VOL. XLIV, NO. 517 JANUARY, 1910

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. The Reappearance in the Offspring of artificially produced Parental Modifications. Dr. FRANCIS B. SUMNER 5

II. A Bimodal Variation Polygon in Syndesmon thalictroides and its Morphological Significance. Dr. J. ARTHUR HARRIS 19

III. The Miocene Trees of the Rocky Mountains. Professor T. D. A. COCKERELL 31

IV. A Suggestion regarding Heavy and Light Seed Grain. L. R. WALDRON . 48

V. Notes and Literature: *Mammalogy*—Nelson's Monograph of the North American Leporidæ, Dr. J. A. ALLEN. *Neurology*—Edinger's Vorlesungen über den Bau der nervösen Centralorgane, Professor G. H. PARKER.

$4.00

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

TO ORNITHOLOGISTS

AND MUSEUMS

W. F. H. ROSENBERG

Importer of Exotic Zoological Specimens

57 Haverstock Hill, N.W., England

Begs to announce the publication of a new Price List (No. 11) of **Bird Skins**. This catalogue contains over 5,000 species, and is the largest and most complete price list of birds ever published. It is arranged in systematic order, based on the classification of the British Museum "Catalogue of Birds," with authors' names, indications of localities, and an index to families. It will be sent gratis and post free on application, as will the following lists:

No. 7, Mammals; No. 8, Birds' Eggs;
No. 9, Reptiles, Amphibia, and Fishes.

Largest stock in the world of specimens in all branches of Zoology.

Specimens sent on approval.

Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

CONTENTS: Introduction, T. C. Chamberlin, Walker Museum; Fifty Years of Darwinism, Edward B. Poulton, Oxford University; The Theory of Natural Selection from the Standpoint of Botany, John M. Coulter, University of Chicago; Isolation as a Factor in Organic Evolution, David Starr Jordan, Stanford University; The Cell in Relation to Heredity and Evolution, Edmund B. Wilson, Columbia University; The Direct Influence of Environment, Dr. D. T. MacDougal, Carnegie Institution of Washington; The Behavior of Unit-Characters in Heredity, W. E. Castle, Harvard University; Mutation, Chas. B. Davenport, Station for Experimental Evolution, Cold Spring Harbor; Adaptation, Carl H. Eigenmann, Indiana University; Darwin and Paleontology, Henry Fairfield Osborn, Columbia University; Evolution and Psychology, G. Stanley Hall, Clark University.

Henry Holt & Company

34 West 33d St., New York
378 Wabash Ave., Chicago

THE AMERICAN NATURALIST

QK1
A427
v.44
1910

THE

AMERICAN NATURALIST

A MONTHLY JOURNAL
DEVOTED TO THE ADVANCEMENT OF THE BIOLOGICAL SCIENCES
WITH SPECIAL REFERENCE TO THE FACTORS OF EVOLUTION

VOLUME XLIV

MO. BOT. GARDEN
1911

NEW YORK
THE SCIENCE PRESS
1910

PRESS OF
THE NEW ERA PRINTING COMPANY
LANCASTER, PA.

THE

AMERICAN NATURALIST

VOL. XLIV January, 1910 No. 517

THE REAPPEARANCE IN THE OFFSPRING OF ARTIFICIALLY PRODUCED PARENTAL MODIFICATIONS [1]

DR. FRANCIS B. SUMNER

WOOD'S HOLE, MASS.

IN a recent paper[2] I have described a series of experiments conducted during the past few years upon white mice. I have there shown that large enough differences of temperature, operating throughout the period of growth, bring about considerable, and in some cases quite obvious, differences in the length of peripheral parts (tail, foot and ear), and probably changes in the quantity of hair as well. The peripheral parts were found to be longer in the warm-room lots (12 to more than 30 per cent. longer, in the case of the tail); the amount of hair, on the contrary, was less. It was pointed out, furthermore, that differences of precisely this sort have long been known to distinguish northern from southern races of mammals.

The question of most vital interest was not, however, touched upon in the earlier paper, although it has furnished my real motive for pursuing these experiments throughout. Are these modifications purely transitory, that is to say confined to the generation immediately affected, or do they reappear, if only to a slight degree, in the offspring? I have long felt that satisfactory evidence for or against the transmission of such modifications would be lacking, so long as zoologists confined themselves to a search for directly visible *qualitative* differences. With few exceptions, however, such has been the method by which the problem has been attacked.

---

[1] This rather cumbersome title has been chosen in order to forestall any possible misrepresentation of my claims by those who do not read beyond headlines. Note that I have used the word "*reappearance*," rather than "*inheritance*."

[2] *Journal of Experimental Zoology*, August, 1909.

The following conditions must, I believe, be realized before we may hope to attain to any satisfactory test of this time-honored question: (1) We must select for experiment such an organism and such a physical agency that the latter may modify the former without directly influencing the germ cells. The action of temperature upon a warm-blooded animal seems to realize this condition most fully. (2) We must discover readily measurable, *quantitative* changes in the parent generation, before we can hope to test the reappearance of such changes in the offspring.

Having discovered such modifications in the parent generation, there are theoretically two methods by which we may attack the problem in hand. We may either (1) raise the offspring of the experimental and control[3] lots under identical conditions, or (2) we may raise the offspring of the modified parents under the same conditions as were employed to effect the original modification. In the first case, we should compare the two sets of animals having different parentage. Assuming a given modification of the value x, and supposing that $1/n$ represented the proportional part of this to be transmitted, the offspring of the two lots would be found to differ by the quantity x/n. If the second method were employed, we should compare the second generation with the parent generation, the two being measured at the same age.

---

[3] For the sake of simplicity I have here assumed that one lot was merely a "control" lot, *i. e.*, exposed to normal or indifferent conditions. In my own experiments, however, I have chosen conditions with a view to modifying both sets of individuals in opposite directions.

Assuming that the latter had been modified to the extent x, the former, according to hypothesis, would be found to be modified to the extent $x + x/n$; *i. e.*, the effect of the conditions would have been cumulative.

Now, as a matter of fact, I have attempted both of these tests upon rather a large scale; but I have not yet found the second one to be practicable, owing to the difficulty, without special facilities, of repeating precisely the same temperature conditions during the lives of two successive generations. But the first test proved to be practicable, and has yielded the results which are summarized in the ensuing paper. Since the full data are to be published elsewhere in the course of the coming year, the omission of certain important portions of the evidence will, I trust, be condoned.

The parents of the mice to be discussed had been divided, at the commencement of life, into two lots, which were reared in separate rooms, differing widely in temperature.[4] Prior to the time of the pairing, they had been exposed to these conditions for an average period of about six months. For reasons which I shall not here state, the two contrasted groups (''warm'' and ''cold'' lots) were not transferred to a common room before pairing.[5] Indeed, the females were not removed to such a room until the time that each was discovered to be pregnant. The discovery was made, on the average, about five days before the birth of the young, *i. e.*, about two weeks after the actual commencement of pregnancy. This circumstance is of possible importance in interpreting the results obtained. On that subject, more anon.

From the time that pregnancy became apparent, the mothers of the two lots were kept in the same room and under conditions which were identical, so far as care could make them so. Differences of temperature were particularly guarded against.

---

[4] Differing by at least 15° C., on the average. The exact figures are not yet computed.

[5] The differences in temperature between the two experimental rooms were, however, very much reduced at this time.

The young were measured at the age of forty-two days. It was found to be impracticable to make certain of these measurements satisfactorily without subjecting the animals to ether. They were not, however, killed at this time. The weight, and the length of tail, foot and ear were determined. The linear measurements were taken with a graduated sliding caliper, indicating tenths of a millimeter. In the case of foot and ear, two measurements were made of each, the mean figure being employed in the computations.[6]

Of these mice, 286 survived to the age of six weeks; there being 141 offspring of warm-room parents, belonging to 33 litters, and 145 offspring of cold-room parents, belonging to 30 litters. From this earlier series of measurements the following gross averages were obtained:

	Weight (grams)	Tail (mm.)	Foot (mm.)	Ear (mm.)
Cold-room descendants	10.897	71.04	17.833	12.434
Warm-room descendants	10.631	71.19	17.960	12.536

It will be seen at once that, although the offspring of the warm-room mice average slightly less in weight, they have slightly longer tails, feet and ears than the offspring of the cold-room mice. These differences are exactly such as were noted, on a larger scale, in the parent generation. But such gross averages do not, in themselves, mean very much. In each of the contrasted groups are comprised individuals of widely different size (the extremes were 6.5 and 19.3 grams). Our material, therefore, is not at all homogeneous.

Accordingly, I have divided the animals into groups, comprising individuals of approximately the same weight.[7] Herewith are presented in tabular form the results of such an analysis.

From the table it will be seen that there are eleven groups in which a comparison between warm-room and cold-room descendants is possible. The mean tail length for the former animals is greater in eight of these eleven cases (exceptions starred); the mean foot-length is greater in nine of the eleven cases; while the mean ear length is greater in nine cases, and equal in one case. Let us consider the likelihood that such results have been obtained through "chance." What are the probabilities that, in tossing a coin, we shall throw "heads" or "tails" as many as eight times out of eleven? The chances that we shall obtain as great an excess as this (on one side or the other) are about 5 out of 22. This is admittedly not a very unlikely happening. The chances that nine of the eleven will be of one kind are about 1 in 15.

---

[6] The average difference between the first and second reading of the caliper was 0.19 mm. for the foot, and 0.12 mm. for the ear.

[7] In my complete table I have likewise dealt with the sexes separately. Lack of space prevents this procedure here.

Group.	Parentage.	Number of individuals.	Weight.	Tail.	Foot.	Ear.
6–6.9 gms.	Cold	2	6.55	59.00	16.950	11.900
	Warm	3	6.77	60.67	16.800*	11.850*
7–7.9 gms.	Cold	12	7.57	61.91 ±0.79	16.954 ±0.110	11.850 ±0.076
	Warm	16	7.58	65.37 ±0.51	17.319 ±0.082	12.037 ±0.047
8–8.9 gms.	Cold	9	8.51	64.78 ±1.23	17.356 ±0.110	12.217 ±0.054
	Warm	19	8.48	67.11 ±0.45	17.642 ±0.052	12.313 ±0.054
9–9.9 gms.	Cold	23	9.41	68.65 ±0.57	17.572 ±0.069	12.311 ±0.035
	Warm	18	9.51	71.29 ±0.30	17.906 ±0.041	12.533 ±0.034
10–10.9 gms.	Cold	32	10.51	71.47 ±0.39	17.962 ±0.069	12.491 ±0.037
	Warm	27	10.33	70.41*±0.47	17.931*±0.050	12.559 ±0.043
11-11.9 gms.	Cold	27	11.42	73.62 ±0.36	17.975 ±0.063	12.534 ±0.0 5
	Warm	17	11.38	73.06*±0.38	17.994 ±0.057	12.568 ±0.085
12–12.9 gms.	Cold	16	12.46	73.37 ±0 66	17.844 ±0.100	12.544 ±0.065
	Warm	18	12.39	73.67 ±0.42	18.122 ±0.052	12.783 ±0.053
13–13.9 gms.	Cold	14	13.31	74.54 ±0.79	18.200 ±0.094	12.629 ±0.069
	Warm	12	13.32	76.33 ±0.46	18.504 ±0.052	12.842 ±0.083
14–14.9 gms.	Cold	3	14.30	75.67	18.333	12.617
	Warm	2	14.20	77.00	18.725	12.700
15–15.9 gms.	Cold	2	15.25	79.00	18.825	12.750
	Warm	6	15.40	77.33*	19.000	13.067
16–16.9 gms.	Cold	3	16.20	79.33	19.100	13.050
	Warm	3	16.37	83.00	19.217	13.050*
19–19.9 gms.	Cold	1	19.30	89.00	19.700	13.200
	Warm	0				

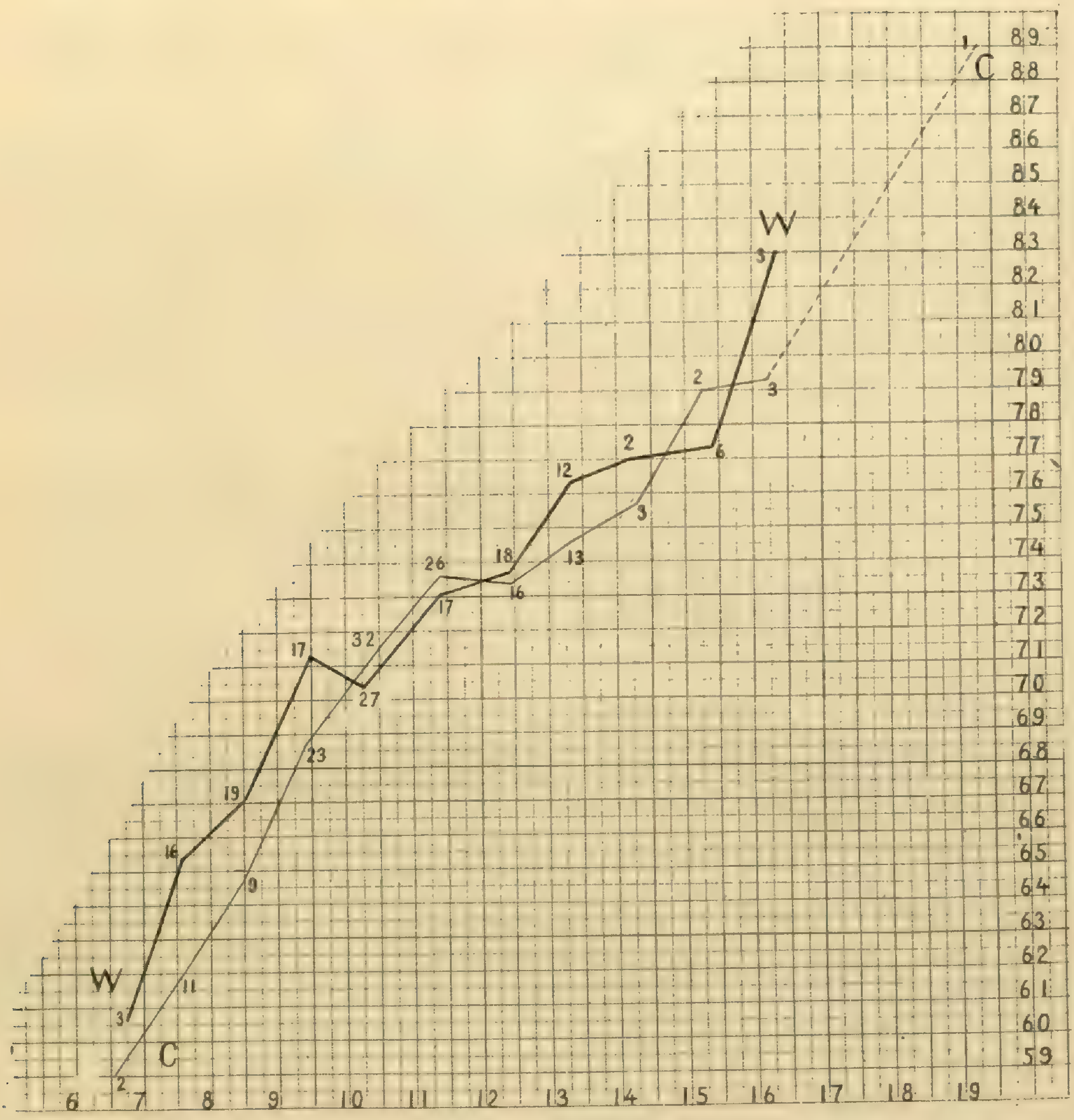


FIG. 1. Curves showing mean tail length in relation to the size of the animals. The heavier line (*W*) represents the condition in the offspring of warm-room parents, the lighter line (*C*) representing that in the offspring of cold-room parents. Abscissas denote weight in grams; ordinates denote tail length in millimeters. The figures along the curves denote the number of individuals in each size-group.

Finally, the chances that we shall obtain as high a proportion as nine out of ten[8] of the same sort are only 2 in 93.

It must be borne in mind, however, that we have the cumulative testimony of these three characters, all point-

---

[8] The group in which the two contrasted lots showed an *equal* ear-length has been left out of account. This would correspond to the case of a coin remaining poised *edgewise*. In our probability estimates we have not contemplated such a contingency.

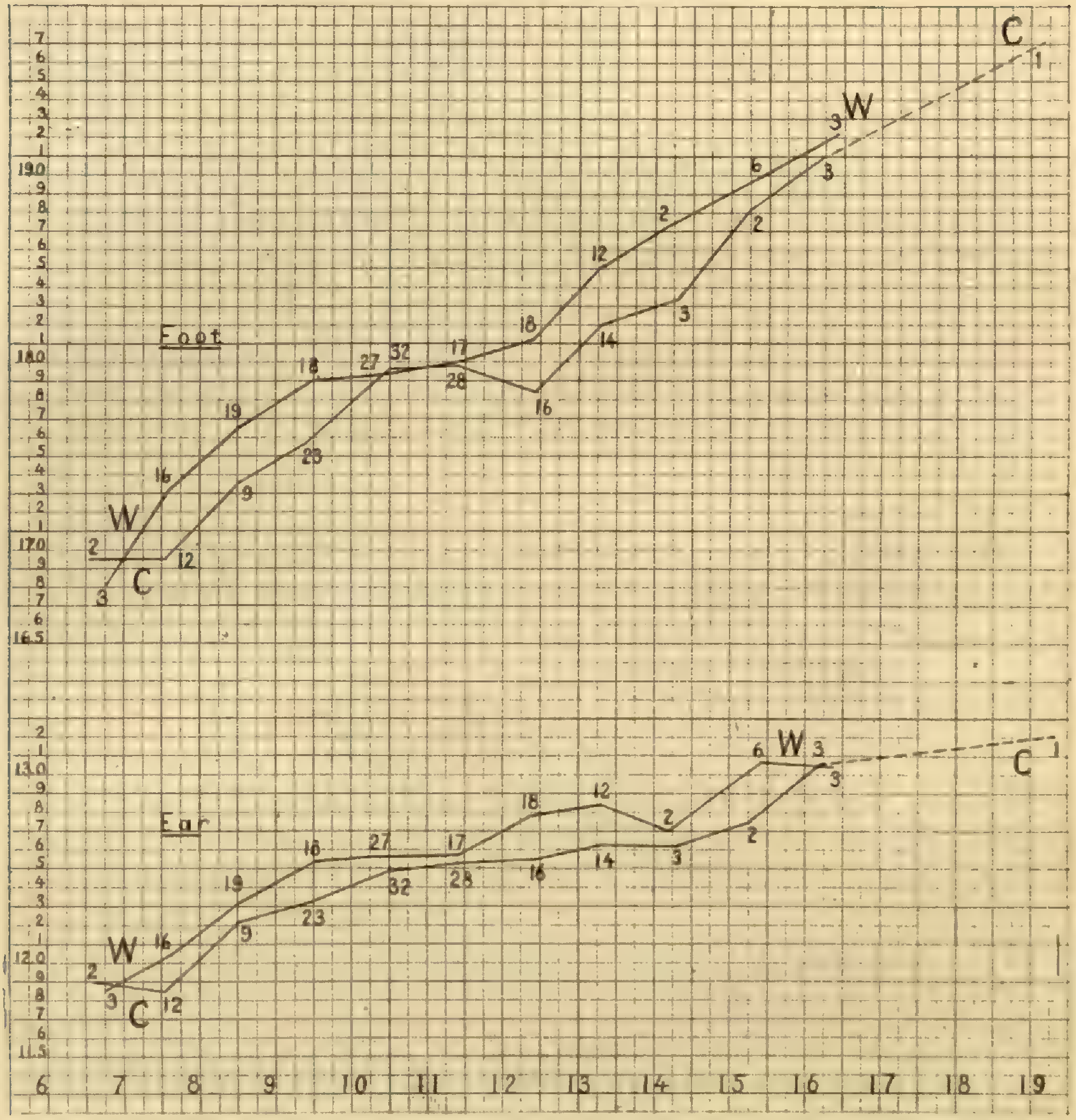


FIG. 2. Curves showing mean foot and ear length. The upper line (*W*) in each case is that showing condition in offspring of warm-room parents. For further explanation see Fig. 1.

ing in the same direction; *i. e.,* we have 26 out of 33 cases showing the same tendency. If we assume that these parts vary quite independently of one another,[9] and if we leave out of consideration the single case of equality, the probability of our obtaining such a large majority in a purely "accidental" way is only 1 in 1,869. In most of the practical affairs of life, we should reject such a contingency as not worth considering.

---

[9] In reality, there is a certain degree of correlation between them, the extent of which has not been computed. This would render the chances somewhat greater than is here indicated.

Thus far, we have treated these groups as of equal value in our computations. From our table it will be seen, however, that the groups differ greatly in respect to the number of individuals comprised, and in respect to the magnitude of the differences shown. I have computed the probable errors of the averages for those seven groups which are large enough to make this worth while. Taking into account the three characters (tail, foot and ear) for the seven groups, we have, accordingly, twenty-one probable errors for each of the contrasted sets ("warm" and "cold"). A little figuring shows that in twelve of these twenty-one cases the difference between two contrasted averages is two or more times as great as the probable error of that difference; in one case the difference is over three times its probable error, and in three cases it is over four times its probable error.[10] The significance of these facts will be appreciated by any one familiar with statistical methods.

Diagrams (Fig. 1 and 2) have been constructed permitting of a comparison between the two contrasted sets of mice, with respect to the mean length of tail, foot and ear, for each of the size groups. These curves explain themselves, and further comment seems unnecessary.

The question naturally arises: How do these differences between the warm-room and the cold-room descendants compare in amount with the differences which were shown by the parents as a direct result of the external conditions? Unfortunately, the data necessary for a direct reply to this question are not at hand, since, in the case of the parents of this particular lot, foot and ear length were not determined at the age of six weeks. I have at hand, however, a set of measurements for a considerable number of mice (80 "cold" + 129 "warm"), which were subjected to substantially the same temperature conditions as were these parents. To determine the extent of the differences, we shall consider, not the differences between the gross averages, for reasons already stated, but the average difference, within each size group, between the "warm" and the "cold" figure. These mean differences, representing the extent of the modification shown at the age of six weeks by mice directly influenced by temperature are:

---

[10] It is important to note that in none of the exceptional cases (*i. e.*, those in which the cold room descendants have *longer* peripheral parts) is the difference between the averages as high as two times its probable error. In one case it is practically equal; in another it is considerably less.

Tail	9.710 mm.
Foot	0.7138 mm.
Ear	0.2021 mm.

Corresponding figures for the warm-room and cold-room descendants with which we have been dealing are:

Tail	1.264 mm.
Foot	0.1890 mm.
Ear	0.1281 mm.

Comparing these two sets of figures, we find that the difference in tail length is 13 per cent. as great in the second case as in the first; the difference in foot length is 26 per cent. as great, while the difference in ear length is 63 per cent. as great! These figures are not offered as expressing, with even a rough degree of approximation, the proportional part of these parental modifications which is handed on to the offspring—even granting that such a transmission occurs. The relative magnitude of these three percentages is particularly surprising, in view of the fact that the tail is the organ which responds most decidedly to the temperature differences, while the ear has been shown to be least affected.[11] It might be argued that the very plasticity of a part, which makes it so responsive to outside influences, might render it correspondingly ill adapted to retaining such impressions permanently.[12] Such speculations are decidedly premature, however.

[11] In my earlier paper I even expressed doubt as to the significance of those slight differences which I did find in the case of the ear. Further observations have, however, lessened these doubts.

[12] It must be pointed out that the tail is far more variable than either the foot or the ear.

Another set of measurements was made with this same lot of mice when they reached the age of three months. By that time the numbers had been considerably reduced by death. There were at the later date 114 of the cold-room descendants, and only 84 of the warm-room descendants. The survivors all appeared to be in good health, however.

In order to exclude the possible influence of suggestion or unconscious bias in determining these rather delicate caliper measurements, I adopted the plan of keeping myself in ignorance as to the parentage of each mouse until the latter had been measured.[13]

I shall not at present enter into as full an account of these later measurements as of the first series. The differences between the gross averages are even less to be relied upon here than in the case of the earlier figures, since the two contrasted lots differed much more in their mean size. The warm-room descendants were somewhat the heavier of the two, having a mean weight of 19.45 grams, as compared with 18.56 grams for the other lot. The body length was also somewhat greater for the former (87.683 mm.) than for the latter (86.703 mm.). For statistical purposes, the animals have been grouped in two different ways: (1) according to weight, as was done previously, and (2) according to body length.[14] The latter method of grouping seems a much fairer one than the first, for it is probable that the length of the appendages is correlated primarily with body length, and only incidentally with weight. The single weight-groups, it may be added, contained individuals which differed from one another by as much as 4 or 5 mm. of body length.

To consider the second of these methods first, the animals were divided into groups, within each of which the individuals differed by less than one millimeter in length. Of these groups there are 15 which allow of a comparison between cold-room and warm-room descendants. Now the "warm" figures for tail, foot and ear are larger than the "cold" figures in 12, 11 and 10 cases out of the 15, respectively. The chances for the "accidental" occurrence of such majorities (in either direction) are roughly 1 in 28, 2 in 17, and 3 in 10, respectively. The cumulative improbability, as regards the three cases, is very high, but the exact chances have not been computed.

---

[13] The animals were put into separate small cages, each bearing an identification mark upon the bottom. These cages were ''shuffled'' by one or another of my colleagues in the laboratory.

[14] The mice were killed at the time of these later measurements. For this reason it was possible to determine the body length with accuracy. This is not feasible with living animals, even when etherized.

The results to be derived from a consideration of the weight groups need not be detailed here. It must be stated, however, that the figures, although showing the same general tendency as those we have considered, are not, in themselves, as convincing as were the earlier ones. Indeed, when the size groups are broken up into subgroups according to sex, the figures, for the males, at least, are somewhat equivocal.

Thus, while the results of these latter measurements on the whole confirm the results obtained earlier in life, they are not as striking as those, and, if taken by themselves, could not be regarded as demonstrative. This is due, in part, to the fact that we are dealing with smaller numbers of individuals. It is probably also due, in part, to the principle of the "leveling down of initial differences," concerning which I have had much to say in my earlier paper. And lastly, it is possible that unconscious bias in the use of the calipers may have somewhat exaggerated the differences shown in the earlier series of measurements, although caution was taken to avoid this.[15]

INTERPRETATION

Aside from delusion or deliberate prevarication on the part of the writer, several interpretations of these results seem theoretically possible.

---

[15] The caliper scale was at all times invisible to me until the points of the instrument were finally adjusted. Personally, I regard any such bias in making these measurements as improbable; but it can not be rejected as impossible.

1. The differences may be due merely to "coincidence" or "accident." The odds against such an occurrence have been shown to be high. Indeed the cumulative improbability that all of these differences have been accidental is enormous.

2. They might have resulted from a slight though constant biasing of the measurements in favor of that result which was calculated to give the greatest personal satisfaction. This possibility, which has already been considered, has been excluded in the case of the second series of measurements.

3. Granting their genuineness, the differences may be due, not to any specific influence (hereditary or otherwise) which has affected the tail, foot or ear directly, but to some general constitutional difference in the offspring of the two sets of parents. In other words, these differences in the length of the peripheral parts may be *correlated* with some constitutional difference of a very general sort. In this connection, it must be admitted that the offspring of the warm-room mice showed a very much higher mortality (40 per cent. between the first and second measurements) than those of the cold-room mice (20 per cent.). The former were likewise somewhat larger, on the average, when measured at the age of three months. Thus there did exist some sort of a constitutional difference. The possibility here considered can not, therefore, be set aside. On the other hand, there is absolutely no evidence in its favor.

4. An explanation closely similar to the last would be that the general stage of development in one lot of mice had been accelerated or retarded as compared with that of the other. We know that the ears and feet of young mice are relatively much larger than those of older ones. It might be contended, therefore, that the warm-room descendants were in a relatively more juvenile condition, despite the fact that they were, on the average, no smaller (*larger,* indeed, at the time of the later measurements).

Even this possibility can not be dismissed without a hearing.

5. The offspring themselves, during their fetal life, may have been influenced in some way by the differences of temperature to which the mothers were subjected during the first two weeks of pregnancy (see above). It is obvious, however, that in a warm-blooded animal, the fetus could not be directly affected by differences of temperature *as such.* It would be curious, indeed, if the parental modifications should be so closely paralleled under these circumstances.

6. The germ-cells of the parents may have been so affected by the external conditions to which the latter were subjected that modifications resulted in the offspring similar to those which were produced in the parents directly. This hypothesis has been invoked again and again to account for a certain class of facts which would seem at first sight to lend strong support to the Lamarckian hypothesis, *e. g.,* by Weismann and by Tower. Such an explanation could not, however, be applied in the present case without radical modification. For we may again point out that in a warm-blooded animal differences of temperature, *as such,* could not affect either the fetus or the germ-cells to any appreciable extent.[16] The suggestion might be made, however, that the effects of temperature, even upon the parent body itself, may not be direct, but may be due to the formation of specific chemical substances which, through the medium of the blood, may be supposed to simultaneously influence the body and the germ-cells. Such a hypothesis can neither be proved nor disproved in the present state of our knowledge, but it is perhaps the type of explanation which is calculated to appeal most strongly to the biologist of to-day. It may be pointed out, however, that *if a mech-*

---

[16] Pembrey (*Journal of Physiology,* Vol. XVIII, 1895, pp. 363–379) found the temperature of adult mice to remain constant at widely different external temperatures. In the young, however (under ten days old), the body temperature was found to vary with that of the atmosphere.

anism exists whereby the germ-cells may be so influenced as to bring about the parallel modification of parent and offspring, such a mechanism would be of exactly the same value for evolution as the "inheritance of acquired characters" in the old sense. For heredity, however, the case would be different. We should still be able to go on talking about the "continuity of the germ-plasm," though that expression would have been shorn of much of its meaning.

7. Finally, we have the view that the changes undergone by the parent body are in some way registered in the germ-cells, so as to be repeated, in a certain measure, in the body of the offspring. The "classical" attempt to make this process intelligible is of course Darwin's hypothesis of "pangenesis." Other views have been put forward recently[17] which are scarcely to be distinguished from the preceding type of explanation (no. 6).

It would not be profitable to enter into any scholastic discussion of these various hypotheses. One after another of these alternatives must be excluded by carefully planned experiments; and it is the intention of the present writer to continue such experiments on a much greater scale in the near future.

November 6, 1909.

[17] *E. g.*, by Cunningham, Archiv für Entwicklungsmechanik, 1908.

A BIMODAL VARIATION POLYGON IN SYNDESMON THALICTROIDES AND ITS MORPHOLOGIL SIGNIFICANCE

DR. J. ARTHUR HARRIS

CARNEGIE INSTITUTION OF WASHINGTON

In the spring of 1906 I had occasion to count the number of leaf laminæ in the involucres of a series of four hundred inflorescences of *Syndesmon thalictroides* collected from the north slope of a hill at Meramec Highlands, Missouri. In making the records, each distinct lamina was counted, whether it was leaf or leaflet, the immediate purpose of the work being to get some idea of the variability in the number of divisions of the leaf surface in the involucral whorl and the degree of interdependence of the number of laminæ and the number of flowers for comparison with studies already made of the correlation between length of stalk and number of flowers per umbel in Nothoscordium and Allium,[1] and between number of flowers per inflorescence and number of ovules or seeds per ovary in Cercis[2] and Celastrus.[3] When I gathered the material I was quite aware that this rough method of lumping the laminæ is not suited to bring out the morphological significance of the data, but only a little time was available for the work and for the purpose then in hand the method of treatment seemed quite adequate.

These data are shown in the form of a correlation surface in Table I.

It is quite unnecessary to publish graphs for these two distributions to show the conspicuously bimodal character. For the number of laminæ, there are conspicuous modes on 4 and 6, and for the number of flowers, pronounced modes on 1 and 3.

---

[1] Harris, J. Arthur, *Ann. Rept. Mo. Bot. Gard.*, Vol. XX, 1909.

[2] Harris, J. Arthur, *Biometrika.* In press.

[3] Harris, J. Arthur, *Ann. Rept. Mo. Bot. Gard.*, Vol. XX, 1909.

Bimodal and multimodal polygons have received so much attention in the literature of variation that the interest of a more detailed investigation was at once apparent. Before considering further our data on this species we may note the more important discussion of these anomalous frequency distributions.

TABLE I

TOTAL LAMINÆ AND TOTAL FLOWERS PER INFLORESCENCE

Flowers per Inflorescence

Laminæ per Inflorescence.	1	2	3	4	Totals.
1	1	—	—	—	1
2	1	—	—	—	1
3	4	1	1	—	6
4	38	25	47	—	110
5	9	18	28	—	55
6	36	22	158	2	218
7	1	1	2	4	8
8	—	—	—	1	1
Totals.	90	69	236	7	400

Bateson[4] gives a bimodal variation polygon for the length of horns in the beetle *Xylotrupes gideon* and the length of the forceps in the earwig, *Forficula auricularia*, but the factors underlying the phenomena are not demonstrated. Naturally the first suggestion concerning a bimodal or polymodal polygon is that there is taxonomic heterogeneity in the material examined. Davenport and Blankenship[5] have even suggested criteria for determining whether the component elements of a two-humped curve are to be designated as "varieties" or "species." So far as I am aware the first attempt to analyze a bimodal polygon into its component elements is that of De Vries[6] with *Chrysanthemum segetum.* Pearson[7] in the first of his "Mathematical Contributions to the Theory of Evolution" deals with the mathematical analysis of composite frequency curves.

---

[4] Bateson, W., "Materials for the Study of Variation," pp. 37–42, fig. 2–3, 1894.

[5] Davenport, C. B., and J. W. Blankinship, *Science*, N. S., Vol. VII, pp. 685–694, 1898.

[6] De Vries, H., *Archiv für Entwickelungsemechanik*, Vol. II, 1895; also *Ber. Deutsch. Bot. Ges.*, Vol. XVII, pp. 84–98, 1899; also "Die Mutationstheorie," Vol. I, pp. 526–529; Vol. II, p. 349.

Dimorphism referable to peculiar environmental conditions has received considerable attention, but unfortunately quantitative data are not numerous. For seasonal dimorphism in Idotheca, Gadzikiewicz[8] has published some figures which yield very different polygons for the body length of September and March females.

The above cases are illustrative merely and make no pretense at completely setting forth the literature.

Ludwig and his pupils have devoted a whole series of papers[9] to the discussion of multimodal variation polygons. De Vries in "Die Mutationstheorie" lays considerable stress upon the Fibonacci series. More recently Ritter[10] and Heyer[11] have taken up the questions and the reader should consult these papers for a full statement of the problems and the pertinent literature. In any discussions in this field, the warnings set forth in papers by Pearson[12] and by Pearson, Yule, Tower and Lee[13] on the sources of apparent polymorphism in plants should always be kept clearly in mind.

Here I do not care to discuss the work of those who conclude that frequency curves have modes where they would be expected in accordance with some mathematical series. It is obvious to any one trained in working with numbers that there are serious difficulties in the way of demonstrating a number of modes in a frequency distribution. The errors of random sampling can not be disregarded and when the variation is continuous instead of discrete the chances of errors due to biased judgment are great. These facts emphasize the necessity for seeking out the simplest possible cases of polymorphism and determining in so far as possible the morphological conditions which underlie them. Such a case seems to be offered by the involucral leaves of Syndesmon.

---

[7] Pearson, K., *Phil. Trans. Roy. Soc. Lond.*, A., Vol. CLXXXV, pp. 71–110.

[8] Gadzikiewicz, *Bull. Acad. Sci. St. Petersb.*, Vol. XXIV, pp. 263–272, 1906; also *Biolog. Centralbl.*, Vol. XXVII, pp. 505–508, 1907.

[9] A complete bibliography of this work is quite out of place here. The reader may consult F. Ludwig, *Biometrika*, Vol. I, pp. 11–29, 1901, for a general statement of some of Ludwig's own views. See also citations by Ritter.

[10] Ritter, G., *Beih. Bot. Centralbl.*, Abth. II, Vol. XXII, pp. 317–330, 1907; Abth. I, Vol. XXIII, pp. 273–319, 1908; Abth. I, Vol. XXV, pp. 1–29, 1909. Rather full citations of the literature are given in these papers.

[11] Heyer, A., *Biometrika*, Vol. VI, pp. 354–365, 1909.

[12] Pearson, K., *Biometrika*, Vol. I, pp. 260–261, 1902.

[13] Pearson, K., G. U. Yule, W. Tower and A. Lee, *Biometrika*, Vol. I, pp. 304–319, 1902. See also a note on a paper by Shull, *Biometrika*, Vol. II, pp. 113–114, 1902.

After I had made my first series of countings a paper by Kellerman[14] giving the essential morphological features of the leaves and considerable statistical data concerning their variation came to my notice. He does not present his data in a form suitable for statistical consideration, and did not note the bimodal condition which appears where a curve is plotted for the entire number of laminæ.

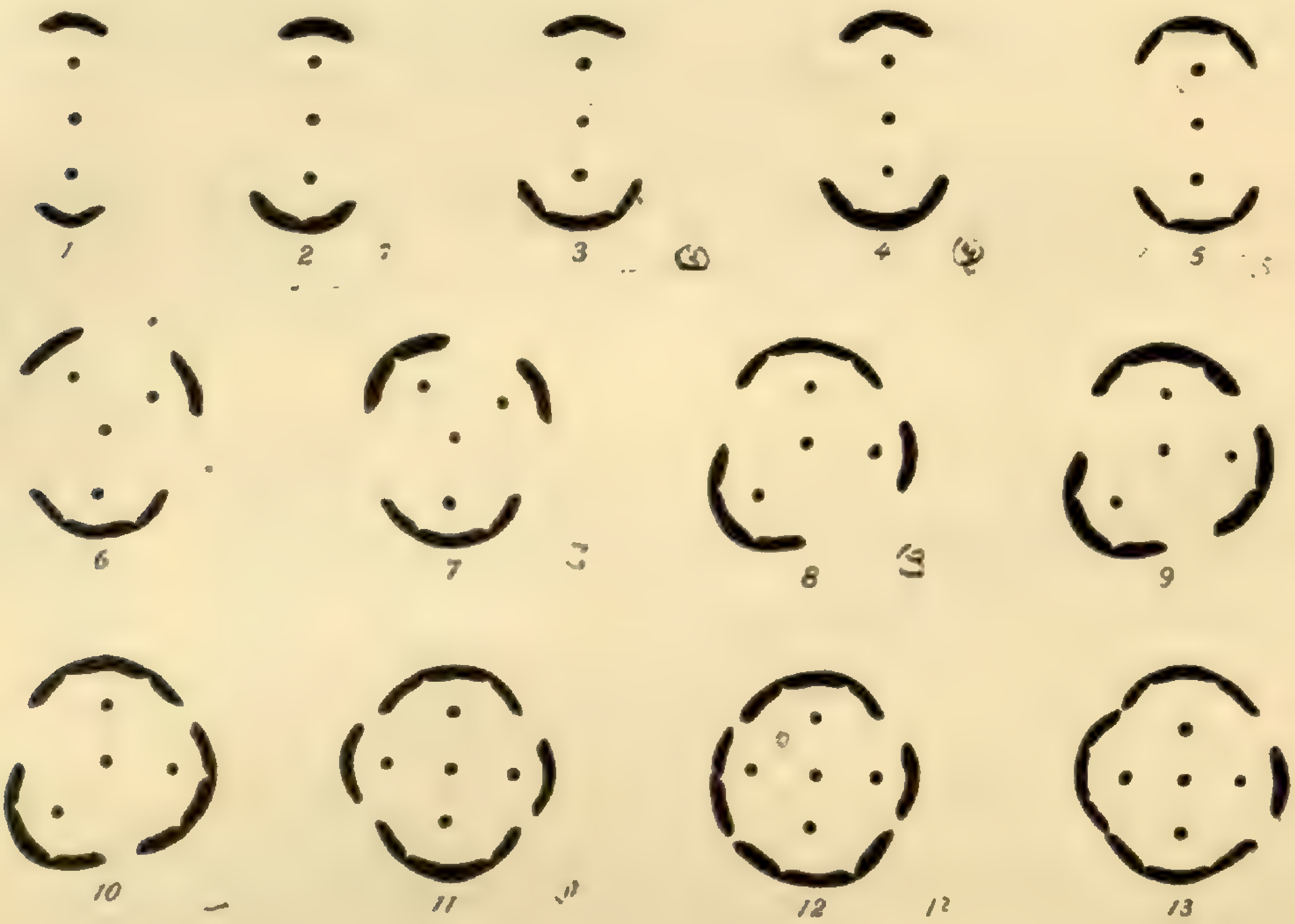
Kellerman's diagrams represent the morphology of the inflorescence very well and are reproduced here with such additional ones as are necessary to represent the types of leaves observed in our series. The terminal and axillary buds which may develop into flower-bearing axes are represented by solid dots. The number of leaflets into which a leaf is divided is indicated by the partial division of the line representing the leaf. Unfortunately Kellerman's data are rather too few to be given further statistical analysis. For figures illustrating the general appearance of different inflorescences the reader may consult his plate.

Most simply the inflorescence consists of a terminal flower, two involucral leaves and two axillary flowers. The axillary buds do not always develop. The leaves may be entire or divided into (generally) three leaflets.

The form of inflorescences with two leaves, one terminal flower and two axillary flowers is shown in Figs. 1 to 5. In our series we find all cases from those with both leaves simple to those with both leaves ternately compound.

---

[14] Kellerman, W. A., *Ohio Nat.*, Vol. I, pp. 107–110, 1901.



Inflorescences of Seq.

In the next group of inflorescences an extra leaf is added. The additional axillary bud thus introduced raises the normal number of pedicels to four. Among the inflorescences with a whorl of three leaves I found none in which at least one of the leaves was not ternately com-

TABLE II

FREQUENCY OF DIFFERENT TYPES OF INFLORESCENCES WITH 2 LEAVES

Class.	*f*	Class.	*f*
1—1—3 (3)	1	3—2—3 (3)	13
1—1—3 (2)	0	3—2—3 (2)	7
1—1—3 (1)	1	3—2—3 (1)	11
Fig. 1		Fig. 4	
2—1—3 (3	0	3—3—3 (3)[15]	297
2—1—3 (2)	2	3—3—3 (2)	95
2—1—3 (1)	1	3—3—3 (1)	74
Fig. 2		Fig. 5	
3—1—3 (3)	9		
3—1—3 (2)	16	Total.	544
3—1—3 (1)	17		
Fig. 3			

pound, but in three of them two of the leaves were simple. The different normal types observed are made clear by diagrams 6 to 10.

TABLE III

FREQUENCY OF DIFFERENT TYPES OF INFLORESCENCES WITH 3 AND 4 LEAVES

Class.	*f*	Class.	
3—1—1—**4** (4)	2	3—3—2—**4** (5)[18]	1
3—1—1—**4** (3)	1	3—3—2—**4** (4)	4
3—1—1—**4** (2)	0	3—3—2—**4** (3)	0
3—1—1—**4** (1)	0	3—3—2—**4** (2)	1
Fig. 6		3—3—2—**4** (1)	0
3—2—1—**4** (4)	1	Fig. 9	
3—2—1—**4** (3)	0	3—3—3—**4** (4)	6
3—2—1—**4** (2)	0	3—3—3—**4** (3)	2
3—2—1—**4** (1)	1	3—3—3—**4** (2)	0
Fig. 7		3—3—3—**4** (1)	0
3—3—1—**4** (5)[16]	3	Fig. 10	
3—3—1—**4** (4)[17]	76	Total.	137
3—3—1—**4** (3)	15	3—3—1—1—**5** (5)	1
3—3—1—**4** (2)	7	3—3—1—1—**5** (3)	1
3—3—1—**4** (1)	17	Fig. 11	
Fig. 8		3—3—2—1—**5** (5)	1
		Fig. 12.	
		3—3—3—1—**5** (3)	1
		Fig. 13	
		Total.	4

Finally, four leaves with the possibility of four axillary pedicels may be found. The condition of the division of these leaves into leaflets is shown in Figs. 11 to 13.

---

[15] We may note four slightly abnormal inflorescences of the 3—3—**3** type. In one there was concrescence of the terminal and one axillary pedicel for some distance from the base. In another one of the axillary peduncles bore a lateral leaf. In a third the central of the three leaflets of one of the leaves was again divided into three secondary leaflets. In the fourth case the two leaves were not opposite, as is usually the case, but were considerably separated on the axis.

[16] In one of these three cases two peduncles are produced from one of the axils. In the other two, one of the axillary pedicels bears a leaf subtending a secondary pedicel bearing the fifth fruit.

[17] In one of these 76 cases the fourth flower is due to one of the lateral pedicels bearing a leaf in the axil of which a secondary pedicel is borne; one of the axillary buds produces no flower in this case. In two other cases one of the axillary pedicels bore a leaf, but no pedicel was produced in its axil. In one of these cases one of the three leaflets—a lateral one—was again divided into two secondary leaflets.

[18] The fifth flower is due to two axillary pedicels being produced from one of the leaves.

Certain "teratological" cases are not represented by figures, but are described merely.

We may now turn to the important question of the frequency of the several morphological types in the Cold Spring Harbor collection made in the spring of 1909.

In classifying these inflorescences all which were injured in any way so that the number of primary divisions of the leaf could not be made out with certainty were discarded. Especial care was used in cases in which a leaf was apparently divided into two leaflets, since such often results from the breaking off of one of the lateral leaflets of a ternately compound leaf. In some cases inflorescences were included in which the laminæ of the primary leaflets were not intact, so that the data can not be trusted for the frequency of secondary divisions. In counting, only completely divided laminæ were considered as leaflets.

Petiolate leaves were not infrequently found, but no special record was kept of them.

The data are set forth in minutely analyzed form in Table II–III. The light-faced numbers separated by dashes represent the number of primary leaflets into which the leaves are divided. The black-faced numbers show the number of flower-buds—terminal and axillary—which might normally have developed, and the number immediately following in parentheses shows the number actually developing. The *f* (= frequency) column gives the number of occurrences of each type.

Grouping the data according to the number of leaves per inflorescence, we find:

Two leaves, in	544	cases.
Three leaves, in	137	cases.
Four leaves, in	4	cases.
	685	altogether.

Here is an example of what De Vries[19] has termed a half-Galton curve. Whether it would be possible to increase the number of leaves by selection as De Vries was able to do in the case of the petals of Ranunculus could only be determined by direct experiment. Possibly the skew curve here found is merely due to the age or vigor of the individuals.

---

[19] De Vries, H., *Ber. Deutsch. Bot. Ges.*, Vol. XII, pp. 197–207. 1894.

Considering next the distribution of the number of primary leaflets per leaf in the material we may seriate the number of leaflets for each class of plants separately, as in Table IV.

TABLE IV

NUMBER OF PRIMARY LEAFLETS PER LEAF IN LEAVES FROM ALL DIFFERENT CLASSES OF INFLORESCENCES

Leaves per Inflorescence

		2	3	4	Totals.
Lobes per Leaf.	1	49	126	6	181
	2	34	8	1	43
	3	1005	277	9	1291
Totals.		1088	411	16	1515

Only sixteen leaves were available for the inflorescences producing four leaves, but for those with two and three leaves the number is ample. In each of the three classes of inflorescences, and in the total, there is a pronounced mode on undivided leaves and on those with three leaflets. Throughout, those with two leaflets are much less frequent than those with either one or three.

Reducing the frequencies for the inflorescences with two and three leaves to a percentage basis for more direct comparison, and laying them side by side in Figs. 14 and 15, we note at once that there is a wide difference in the proportion of single leaves in the two series. The source of this difference is at once clear. In the inflorescences with the third leaf, the additional leaf is nearly always simple. Thus the proportion springs at once from about 4.5 per cent. to 30.5 per cent.

Unfortunately, our data, though extensive, are not numerous enough to permit of further analysis. If material were more ample it might be possible to ascertain more precisely some of the factors determining the condition of division of the leaf. All that we can conclude from the present data is that: (*a*) There is a strong tendency to the production of either simple or ternately compound leaves—those divided into two leaflets are rare; (*b*) a larger proportion of the leaves are simple in inflorescences with three or four leaves than in those with but two leaves.

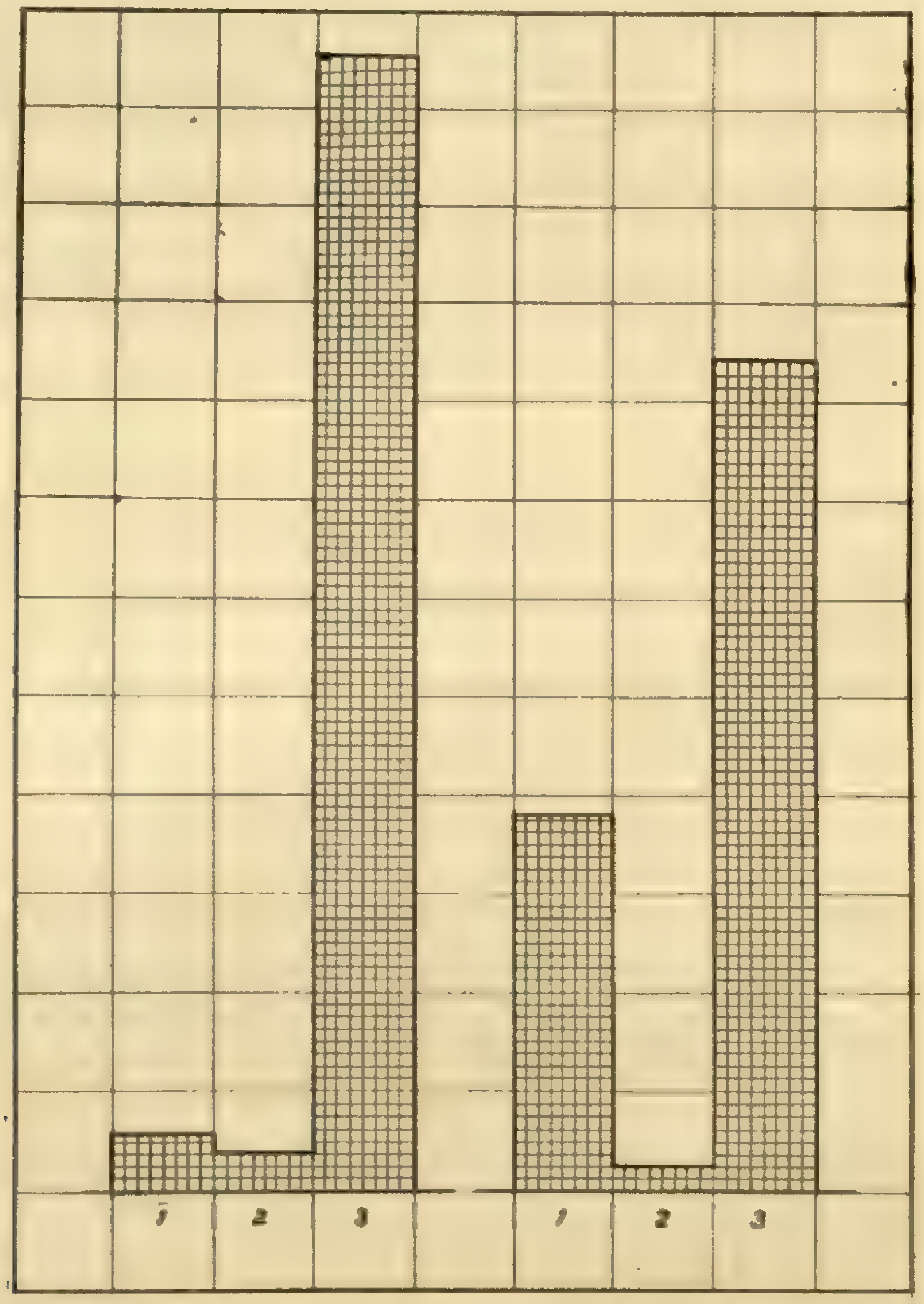


FIG. 14. FIG. 15.

To determine whether the distribution for number of leaf laminæ per involucre in this series forms a bimodal distribution similar to that found in 1905, I extract the totals from the two tables of data. To ascertain more accurately the real source of the bimodal condition, should it be found to exist in this series, the combinations which give rise to the different total numbers are given in Table V.

From these figures appear several points which could not be determined at all on the lumped data as collected in 1905.

The grand total shows that there is a slight empirical mode on four and a conspicuous one on six laminæ, as compared with the very prominent modes on these two grades in 1905. The distributions from the three classes of inflorescences shows the origin of these modes very clearly. The mode on four is due entirely to the tendency to the production of one ternately compound and one simple leaf. Both of these types of leaves have been shown to be much more frequent than those divided into two leaflets. The mode on six is due to both of the involucral leaves bearing the modal (three) number of leaflets.

TABLE V

SHOWING THE FREQUENCY AND MODE OF ORIGIN OF THE DIFFERENT TOTAL NUMBERS OF LAMINÆ PER INFLORESCENCE

Laminæ of Individual Leaves

	Two Leaves.						Three Leaves						Four Leaves.				
Total Laminæ per Inflorescence.	1—1	2—1	3—1	3—2	3—3	Totals.	3—1—1	3—2—1	3—3—1	3—3—2	3—3—3	Totals.	3—3—1—1	3—3—2—1	3—3—3—1	Totals.	Grand Totals.
2	2					2											2
3		3				3											3
4			42			42											42
5				31		31	3					3					34
6					466	466		2				2					468
7									118			118					118
8										6		6	2			2	8
9											8	8		1		1	9
10															1	1	1
	2	3	42	31	466	544	3	2	118	6	8	137	2	1	1	4	685

In the 1905 series inflorescences with seven leaflets formed only 2 per cent. of the population; in the 1909 lot they are over 17 per cent. of the total number. There is no way of determining absolutely why there is such a difference, but it seems quite logical to suppose that in the Cold Spring Harbor series inflorescences with three leaves were much more abundant than in the Meramec Highlands lot, for the frequency of seven laminæ in the Cold Spring Harbor material is entirely due to flowering stalks with three leaves of which two are ternately compound and the third undivided.

In the 1905 series all the laminæ found in the inflorescence were included in the countings. In the discussions just given I have treated only the primary leaflets. The data for the other laminæ are included in the notes on the tables of data or in the notes on teratological cases. Their addition would make little difference in our distributions, but the data are available for any one who cares to use them.

TABLE VI

Seriation of Number of Flowers Developing in Different Types of Inflorescences

		Leaves per Inflorescence			
		2	3	4	Totals.
Flowers per Inflorescence.	1	104	18	—	122
	2	120	8	—	128
	3	320	18	2	340
	4	—	89	—	89
	5	—	4	2	6
		544	137	4	685

Further analysis of the data for leaf characters is not justified by the quantity of material. Two conclusions are seen to be amply justified by the facts: (*a*) In Syndesmon there is a strong tendency to the production of simple and trifoliate leaves. (*b*) The preceding fact, taken in connection with the peculiarities of the inflorescence with regard to the number of leaves produced, is quite sufficient to account for the bimodal condition of the variation polygon for number of laminæ per inflorescence.

The bimodal polygon is therefore explicable on purely morphological grounds without any assumption of the mixture of two or more "races" or "minor species," provided the plants producing two, three and four leaves per inflorescence be not considered "small species" or "biotypes." Personally I see no reason whatever to think that they are, but in these days of minute segregation the possibility must not be left unmentioned. To me it seems not unlikely that the three different classes of inflorescences noted are to some extent to be referred to age differences in the individuals producing them.

The number of flowers developing may now be tabulated for each of the three classes of inflorescences. The results are given in Table VI.

Here the bimodal condition in the number of flowers per inflorescence found in the 1905 series does not appear, although the frequency of inflorescences with one flower is about as great as that of those with two. Doubtless the reason for this difference would be clear if we had as complete information concerning the 1905 series as is available for the 1909 material.

The purpose of the present note will have been fulfilled if in addition to the recording of a mass of definite quantitative data concerning the form of the inflorescence in Syndesmon, it convinces students of variation of the importance of a critical consideration of purely morphological features before concluding that an empirical multimodal polygon indicates the existence of biotypes.

Cold Spring Harbor, L. I.

THE MIOCENE TREES OF THE ROCKY MOUNTAINS

PROFESSOR T. D. A. COCKERELL

UNIVERSITY OF COLORADO.

THE living arborescent flora of the Rocky Mountain region is at the present time occupying the attention of a number of able workers, including Nelson in Wyoming, Rydberg of the New York Botanical Garden, Sudworth of the Forest Service, Ramaley, Bethel and Schneider in Colorado, Wooton in New Mexico, and others. As a result of all this activity, we are promised two manuals of Rocky Mountain botany, and a third of trees alone, so we shall have three separate and independent treatments of our woody flora to compare and choose from.

Unfortunately, those who have been so active and exhaustive in their investigations of the living flora have not cared, as a rule, to consider the historical or paleobotanical side of the subject. Many "recent" botanists seem to have a positive dislike for fossil plants, and few manifest any great eagerness to receive information about the ancestors or predecessors of the species which occupy their attention. Like all enthusiasts, the writer is filled with the idea that the matter has only to be adequately presented to command universal attention; and hence offers this discussion, not so much for the paleobotanists as for those students of living plants whose active interest may be aroused in the problems involved.

Going back from the present time, we are practically without information concerning the plants of our region until we come to the Florissant beds, assigned to the Miocene. These beds, however, contain an abundant series of remains, many of the plants beautifully preserved, as the accompanying illustrations show. They testify to a climate both warmer and damper than that of the present day, the arborescent genera including Sapindus, Ficus,[1] Diospyros, Persea, Leucæna, Anona, etc., but so far as known no palms. Some, as *Ailanthus americana,* pertain to genera now restricted to Asia.

---

[1] The determination of *Ficus* is based on the leaves. In confirmation of

The determination of the age of the Florissant beds has been a matter of some difficulty, notwithstanding the large number of organisms preserved. Comparing the flora with that of the European Tertiary, I have felt satisfied that it should be referred to the Miocene, and probably to the Upper Miocene. The resemblance to the flora of Œningen in Baden, known to be upper Miocene, is most striking. Thus we have the following parallel or representative species:

Florissant.	*Œningen.*
Liquidambar convexum Ckll.	*Liquidambar europæum* A. Br.
Ulmus braunii Heer, Lx.	*Ulmus braunii* Heer.
Comptonia insignis (Lx.) Ckll.	*Comptonia œningensis* A. Br.
Porana speirii Lx.	*Porana œningensis* A. Br.
Porana tenuis Lx.	*Porana macrantha* Heer.
Acer florissanti Kirch.	*Acer tricuspidatum* A. Br.[2]

Many others could be cited. On the other hand, the Florissant incense cedar, *Heyderia* or *Libocedrus coloradensis* Ckll., is to be compared with *H. salicornioides,* of the Lower Miocene of Radoboj in Croatia. The Florissant redwood, *Sequoia haydeni* (Lx.), is not related to *S. sternbergi* Heer from Œningen, but to *S. langsdorfii* (Brgt.) Heer of the Swiss Lower Miocene; this species, however, survived into the Upper Miocene in Italy and Galicia. This *S. langsdorfii* has been recognized in America also from the Upper Cretaceous to the Miocene, and some of the Florissant specimens have been referred to it; but the identity of the plants from so many diverse localities and horizons is questionable, and from Florissant I think we have only one species, *S. haydeni.*

The Sequoia and Libocedrus of Florissant are both very closely related to their living Californian allies; so

---

it comes a discovery by Mr. Brues, who in working over the parasitic Hymenoptera from Florissant has come upon what appears to be a genuine fig-insect, apparently of the South American genus *Tetrapus* Mayr.

[2] *Acer trilobatum* (Sternb., 1825) A. Br., 1845; not *A. trilobatum* Lam., 1786.

much so that one is in some difficulty to point out any tangible differences. This is equally true of a number of other cases, of which the following are illustrative:

Florissant.	*Living.*
Pinus wheeleri Ckll.	*Pinus flexilis* James.
Pinus sturgisi Ckll.	*Pinus tæda* L.
Ailanthus americana Ckll.	*Ailanthus glandulosa* L.
Sambucus newtoni Ckll.	*Sambucus arborescens* Nutt.
Anona spoliata Ckll.	*Anona glabra* L.
Robinia brittoni Ckll.	*Robinia pseudacacia* L.
Populus lesquereuxi Ckll.	*Populus angustifolia* James.
Quercus lyratiformis Ckll.	*Quercus lyrata* Walt.
Sapindus coloradensis Ckll.	*Sapindus drummondi* H. & A.

So numerous are the resemblances to the living flora that one might well feel persuaded to refer the beds to the Pliocene—certainly better there than to the Oligocene or Eocene! However, the Florissant fishes, with the exception of Amia, are of extinct genera, and no less than 178 genera of insects are supposed to be extinct. For a variety of reasons, based chiefly upon a study of the insects, I believe that the Florissant period corresponds with Osborn's "Fifth Faunal Phase" (Bull. 361, U. S. Geol. Survey), in which a new fauna was invading the country from Eurasia, while connection with South America had not yet been established. Some of the Florissant groups of insects, such as the Aphididæ and Bombyliidæ, seem to represent the original American fauna uncontaminated; while others show old world types, the most significant and interesting of which is the tsetse fly (*Glossina*).[3] Osborn's "Fifth Phase" includes the Middle and Upper Miocene, and so far as may be judged, Florissant should belong near the middle of it.

The attempt to correlate the Florissant beds with other American floras ascribed to the Miocene brought out a number of difficulties. With the exception of the little-

---

[3] A second species of tsetse fly, *Glossina osborni* Ckll., has been recently discovered. It is only 10½ mm. long, the wing 7 mm.; the venation is normal for the genus, but the first basal cell bulges less subapically than in Scudder's species.

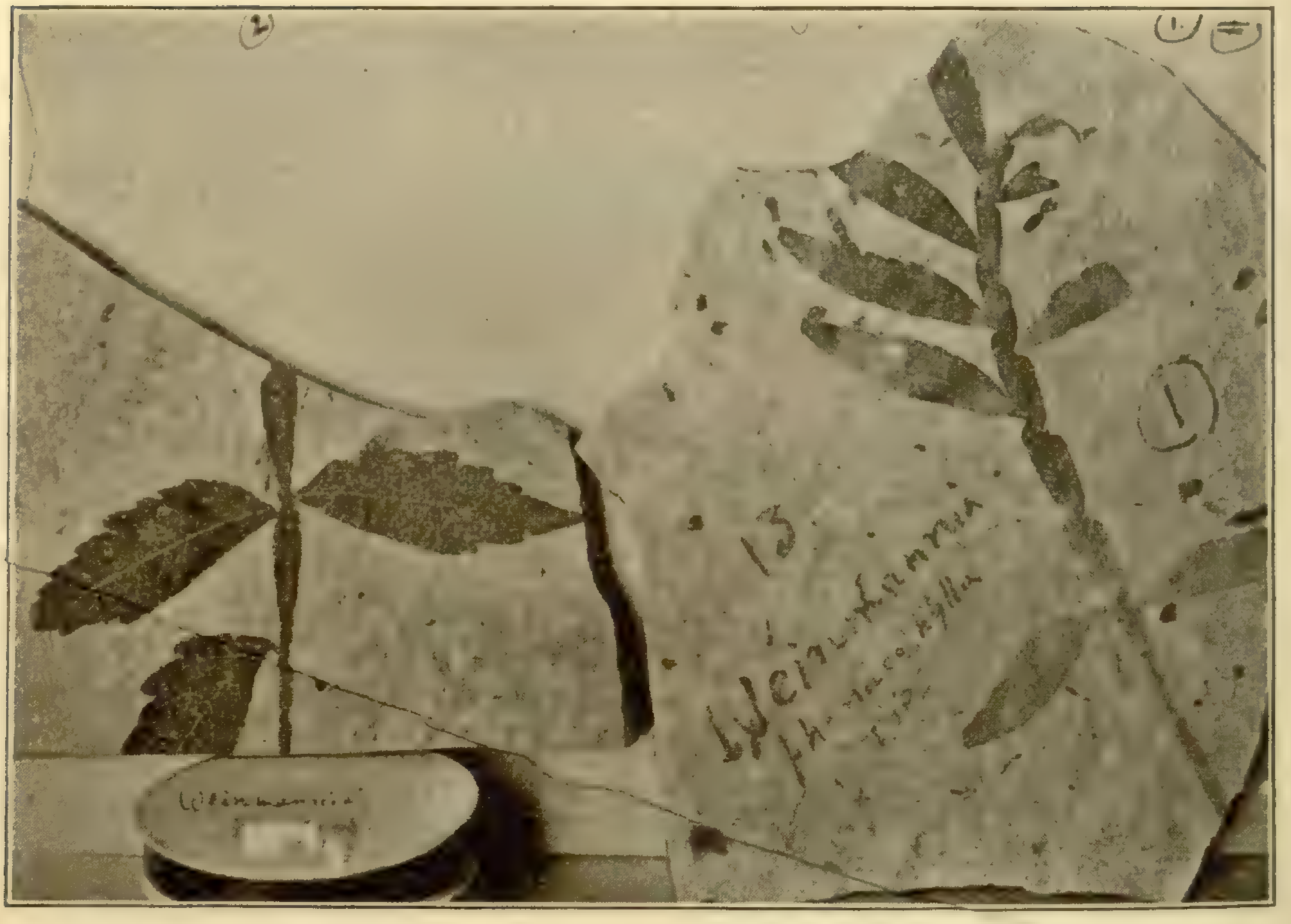


FIG. 2. *Weinmannia lesquereuxi* Ckll. FIG. 1. *Weinmannia phenacophylla* Ckll.

known formation at Elko Station, Nevada, I do not find anything which really seems to correspond with Florissant. According to the theory outlined above the Mascall beds of Oregon, which possess a varied flora, should be either contemporaneous or (more probably) somewhat earlier. Fortunately, fourteen species of mammals have been obtained from the Mascall, and these place it rather definitely in the Middle Miocene. Considering, therefore, a probable moderate difference in time, combined with noteworthy geographical and altitudinal differences, we ought to find the Mascall flora similar to, but by no means identical with, that of Florissant; and this is exactly what comparisons show.

Thus of the 77 Mascall plants (nearly all trees) referred to definite genera, no less than 56 are congeneric with those of Florissant. Of those not congeneric, five are so dubious that they have not been specifically determined. The Mascall genera not yet found at Florissant are the following:

1. *Equisetum.*—This has no significance, as it abounds in Colorado to-day, and must have been present during the Florissant period.

2. *Ginkgo.*—Represented in the Mascall by a fragment not specifically determined. This genus is not known in the Rocky Mountains later than the Laramie and Livingston, on the border line between the Cretaceous and Tertiary. As is well known, there is a single living (Asiatic) species.

3. *Thuites.*—A fragment not specifically determined. It is practically identical with *T. ehrenswärdi* Heer (Miocene of Sachalin and Spitzbergen), but that plant appears to be referable to the modern genus Chamæcyparis.

4. *Glyptostrobus.*—A genus still living in China. It was supposed to occur at Florissant, but I believe the material so referred all belongs to Sequoia. The Mascall material is not above suspicion of also being Sequoia; indeed Lesquereux so referred one of the specimens.

5. *Taxodium.*—The Mascall specimens are referred by Knowlton to the widely distributed *T. distichum miocenum* Heer, which should be called *Taxodium distichum dubium* = *Taxodium dubium* (Sternb.) Heer, originally described from Bilin. This differs from Sequoia by the deciduous leaves, which are not decurrent at the base as in Glyptostrobus. The genus still lives in our southern states.

6. *Artocarpus.*—Represented by very fragmentary material, doubtfully referred to *A. californica* Kn.

7. *Magnolia.*—Major Bendire collected a plant which Knowlton says "may well be" *M. inglefieldi* Heer. It has not been obtained by recent collectors. *Magnolia dayana* Ckll. ined. (*M. lanceolata* Lx. 1878, not Link. 1831) is listed by Knowlton as from the Mascall, but in his detailed account he says it is from Cherry Creek, which should be Lower Eocene.

8. *Laurus.*—Florissant has a species of Persea; Laurus and Persea are allied, and not distinctly separated by paleobotanists.

9. *Platanus.*—The Mascall specimens appear to belong

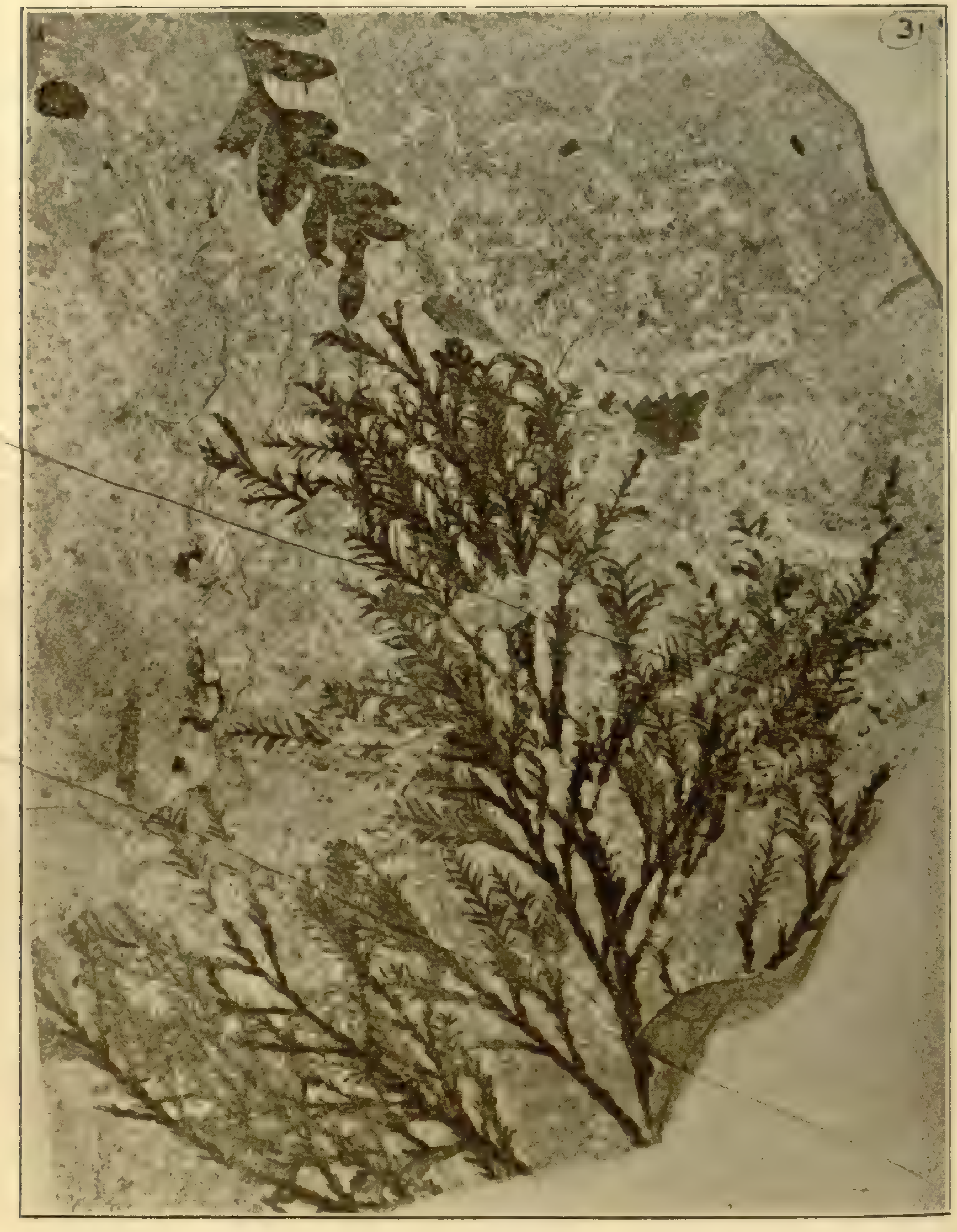


Fig. 3. *Sequoia haydeni* (Lesquereux). Redwood.

to three species, but none are sufficiently well preserved for positive specific identification.

10. *Prunus.*—The two Mascall species described by Knowlton are only doubtfully referred to this genus, which is of course abundant in the modern flora.

11. *Rulac.*—Generic reference rather uncertain; the genus is scarcely separable from Acer, which occurs at Florissant.

12. *Æsculus.*—This well-known living genus is repre-

sented in the Mascall by leaflets which closely resemble an undescribed Florissant species which may be a Berberis, but is certainly not an Æsculus.

13. *Grewia.*—The Mascall plant is referred by Knowlton to *G. crenata* (Unger) Heer, which occurs in Europe at Œningen.[4]

Three other genera, Phragmites, Cyperacites and Smilax, are non-arborescent, and have no particular significance.

Thus it would appear that in the Middle Miocene period Ginkgo and Glyptostrobus—if we may accept the determinations—had not yet retreated from the American continent, but survived at least in the northwest. For the rest, the Mascall flora is no doubt a lowland one as compared with that of Florissant, and this alone would explain many of the differences; thus, no one would expect to find Taxodium growing around a mountain lake.

Dr. Knowlton has described (Monog. U. S. Geol. Survey, Vol. 32, part 2) an extensive flora from the Yellowstone, which he regards as Miocene. The fossil plants of the Yellowstone National Park are divided by him into three series: (1) Fort Union, which is Basal Eocene, (2) Intermediate, said to be Miocene, and (3) Lamar Flora, also Miocene. With the first we are not now concerned, but the others must be compared with the flora of Florissant. Considering the relative proximity of the Yellowstone beds to those of Colorado, one would expect to find much similarity and even identity in the plants; but this is not the case. The difference of locality, with a moderate difference in time, might perhaps account for the diversity of species; but the Yellowstone flora as a whole does not impress one as being so modern as that of the Mascall beds or Florissant, while there is a significant *identity of species* with those of the Eocene.

I have extracted from Knowlton's tables a list of all the Yellowstone "Miocene" plants said to occur elsewhere or in the Eocene, with the following result:

---

[4] The African *Grewia crenata* Hochst., 1868 (not Unger, 1850), takes the name *G. populifolia* Vahl, 1790.

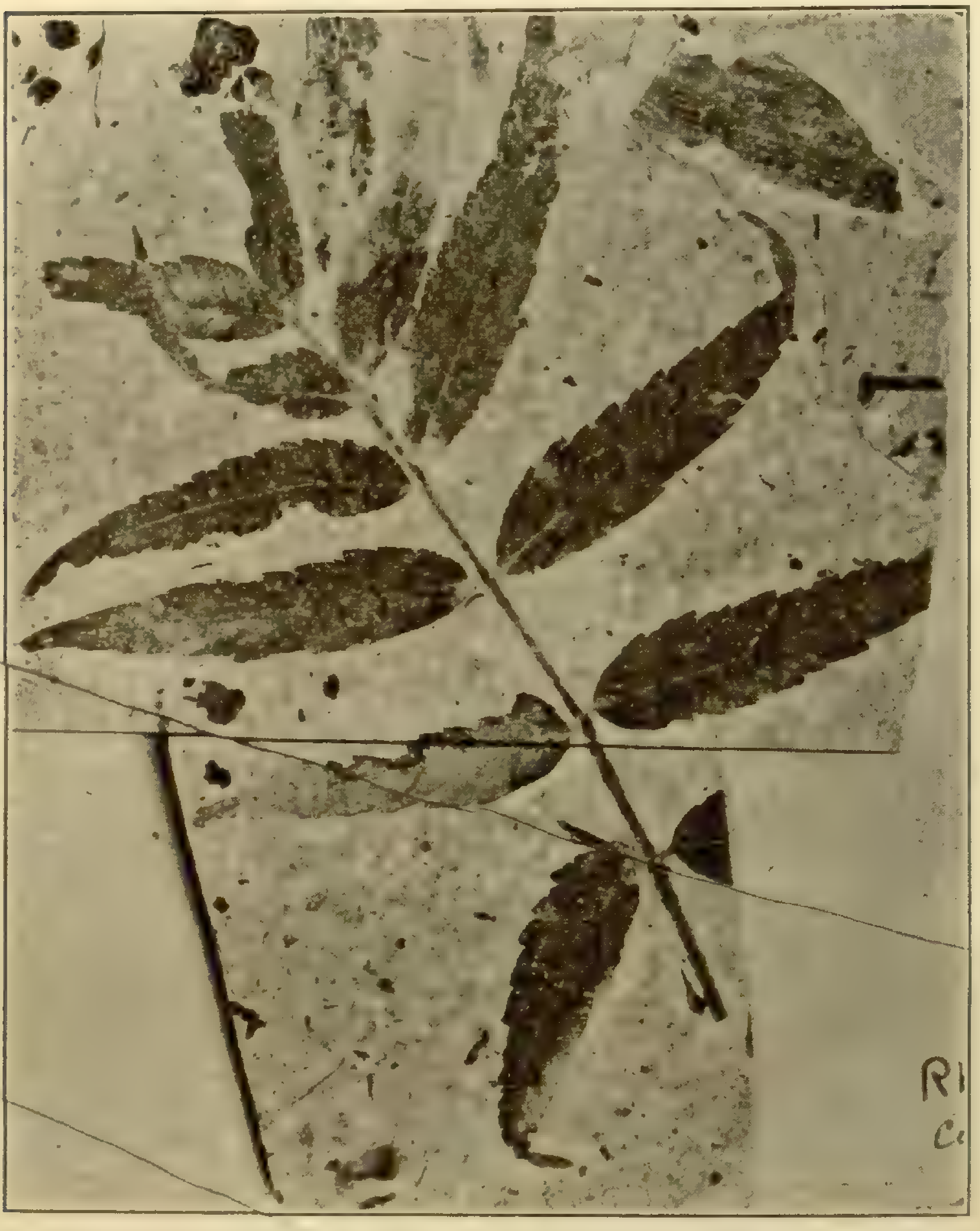


Fig. 4. *Rhus coriarioides* Lesquereux. Sumach.

1. Common to Fort Union (Eocene), Intermediate and Lamar.

    Sequoia langsdorfii (Brgt.). Said to go down to the Laramie (Cretaceous).
    Juglans rugosa Lx. Goes down to the Laramie.
    Castanea pulchella Kn.
    Ficus densifolia Kn.
    Laurus californica Lx. Also auriferous gravels of California.
    Laurus grandis Lx. (not Wallich). Also auriferous gravels of California.
    Platanus guillelmæ Göpp. Perhaps also Laramie.
    Aralia notata Lx. Also Denver beds.
    * *Elæodendron polymorphum* Ward.

2. Common to Fort Union and Intermediate.

    Equisetum canaliculatum Kn. Perhaps also in the Lamar.

Magnolia (?) *pollardi* Kn.
* *Ulmus minima* Ward?
Sapindus affinis Newby.

3. Common to Fort Union and Lamar.

Asplenium iddingsi Kn.
Lygodium kaulfussi Heer.
Equisetum deciduum Kn.
Juglans crescentia Kn.
Ficus asiminæfolia Lx. Also auriferous gravels of California.
Laurus primigenia Unger?
Malapœnna lamarensis Kn.
Sapindus grandifoliolus Ward.
Sapindus wardii Kn.
* *Hicoria antiqua* (Newb.).
**Ulmus pseudofulva* Lx.?

Those marked with an asterisk occur in the Fort Union only outside of the Yellowstone.

4. Common to the Intermediate and the Denver beds (Basal Eocene).

Osmunda affinis Lx.

5. Common to the Lamar, Basal Eocene and Laramie.

Rhamnus rectinervis Heer, Lx. Heer describes this from Monod, in the Lower Miocene; we may venture to doubt the identity of the American plant.

Thus we have twenty-six plants *specifically* identical with those of the Basal Eocene.[5]

6. Common to Lamar and "Green River" of Knowlton. (See also under 7.)

Salix elongata O. Web. Said to occur at Elko Station, Nevada, but represented only by uncharacteristic fragments. The determination of

---

[5] The Mascall is supposed to have five species common to the Fort Union; but of these two are doubtful, two others are the conifers *Sequoia langsdorfii* and *Taxodium*, while the fifth is *Sapindus obtusifolius*, to which a single specimen from the Mascall "seems to belong." *S. obtusifolius* was originally described from beds supposed to belong to the Washakie (Later Eocene).

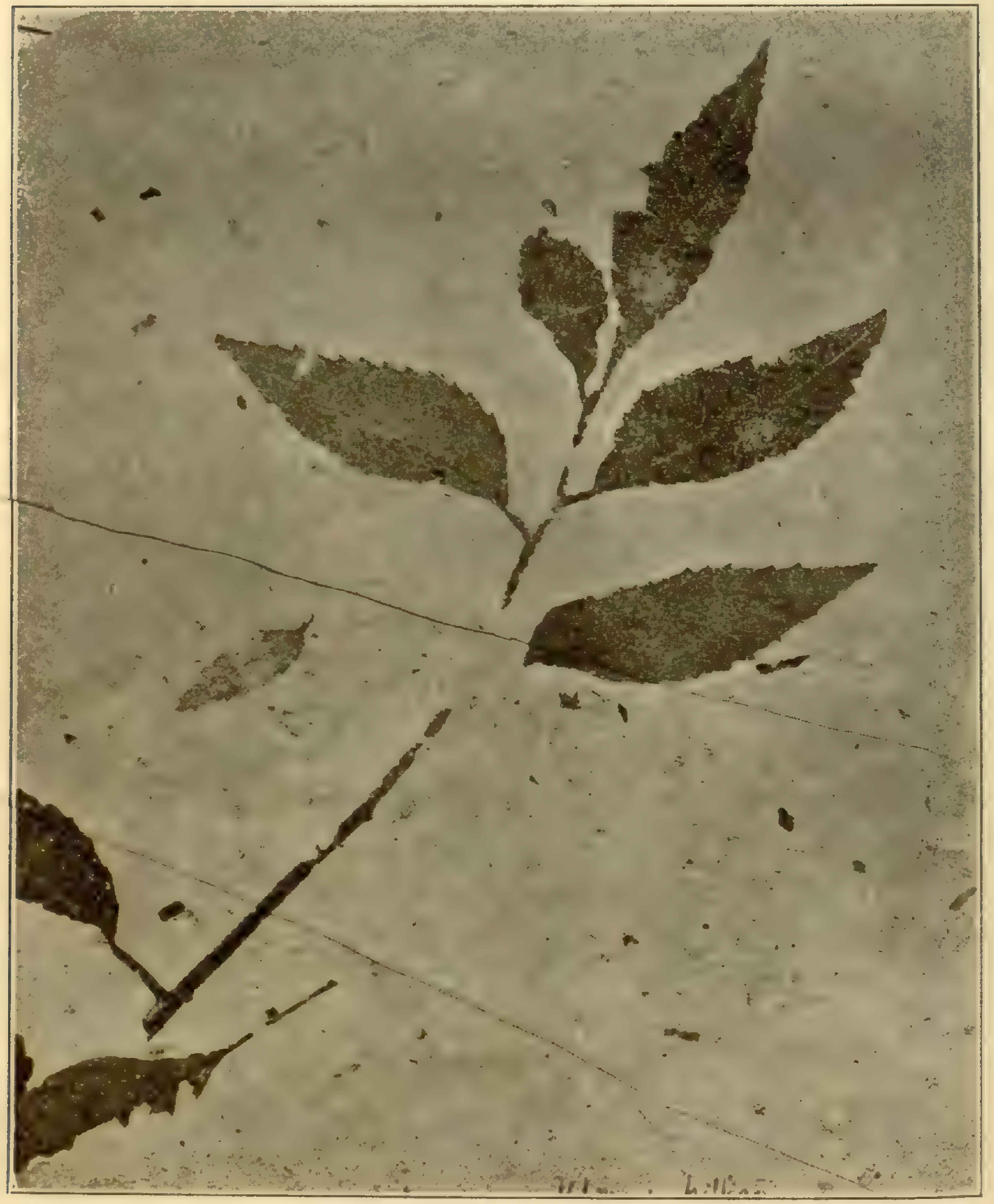


FIG. 5. *Ulmus hilliæ* Lesquereux. Elm.

the Lamar plant is considered doubtful by Knowlton.

Fagus (*Fagopsis*) *longifolia* (Lx.). Elko Station, Nevada; Florissant (very abundant) and Eocene (?) of British Columbia. The British Columbia locality is on the Similkameen River, whence come various fossil insects. Dr. Dawson (quoted by Scudder) considered these deposits Miocene. The Yellowstone collection includes about forty specimens which Knowlton refers here, all from Fossil Forest Ridge. This is, undoubtedly, a distinctively Miocene plant, and must be accepted as pertinent evidence. The determination must be presumed to be correct, though it may be pointed out that various other leaves have almost exactly the same venation and appearance. This is especially true of the species of Zelkova, to which genus Engler (1894) actually referred *F. longifolia,* though the discovery of the fruit has since shown that it is not related thereto. *Ulmus plurinervia,* as figured by Heer from Alaska, is also almost exactly like *F. longifolia;* it is considered doubtfully Eocene, but Knowlton has recognized it in the Mascall (Miocene). From the shape of the base, and other features, it seems to me certain that the Alaskan plant is not the original *U. plurinervia,* of which Unger gives four figures in the Chloris Protogæa. The latter is decidedly more elm-like in appearance.

Corylus macquarrii (Forbes) Heer. This plant, as recognized in America, is a Fort Union and possibly Laramie species; recorded also from the Eocene (?) of Alaska.

Diospyros brachysepala A. Br. As recognized in this country, this is a Laramie and Fort Union species; the record from Florissant I believe to be erroneous.

None of the above belong to the genuine Green River series; three are quite without significance as indicating Miocene affinities, but the *Fagus* stands out as a solitary Miocene representative.

7. Common to the Lamar and the Auriferous gravels of California. (See also under 1 and 3.)

Juglans leonis Ckll. Two specimens in the Lamar.

Populus balsamoides Göpp. Also Miocene (?) of Alaska. Known in the Yellowstone only from a fragment, which certainly can not be positively determined as *balsamoides:* in fact, it shows

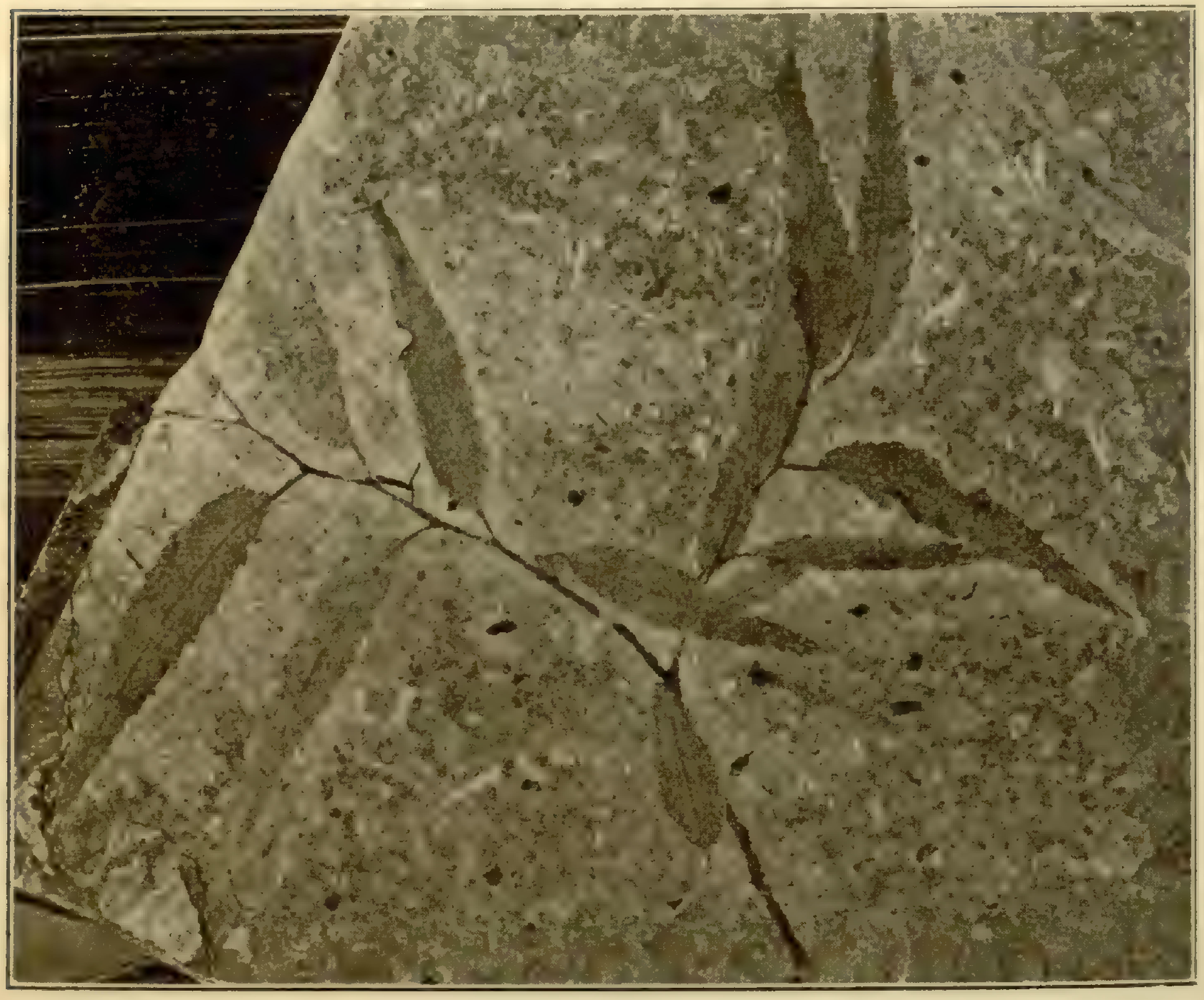


Fig. 6. *Myrica drymeja* (Lesquereux).

some differences, at least as compared with the original European *balsamoides*, which ought to be specific.

Salix varians Göpp. Eocene (?) of Alaska. The Lamar plant is a fragment, and according to the figure, the margin is quite unlike that of the European *varians*.

Salix angusta A. B. Said to occur also in the Basal Eocene and true Green River. The Lamar material consists of doubtful fragments.

Quercus furcinervis americana Kn.

Ficus shastensis Lx.?

Ficus sordida Lx. A mere fragment from the Lamar.

Ficus asiminæfolia Lx. Very indifferent material from the Lamar. Also Fort Union.

Magnolia californica Lx.? The Lamar plant is represented by a single specimen, "so much broken that its positive identification is not possible" (Knowlton).

Persea pseudocarolinensis Lx. The Lamar specimen figured, "the best one found," consists of the upper half of a leaf; what there is of it appears to agree with the Californian species, although it has more lateral viens.

Rhus mixta Lx.?

Aralia whitneyi Lx. Also in the Intermediate. None of the Yellowstone specimens are perfect, but they appear to belong to this handsome species.

Thus the species common to the Lamar and Auriferous gravels, *but not known from Basal Eocene*, are few, and in several cases of doubtful identity. As the reference of the Lamar to the Miocene rests wholly on the resemblance of the flora to that of the Auriferous gravels, with the exception of the indication afforded by *Fagus longifolia*, it must be considered at least somewhat dubious. It is also to be remarked that eleven species of plants are supposed to be common to the Yellowstone Fort Union and the Auriferous gravels, although two of these, at least, are doubtfully from the gravels, while in four or five cases the Yellowstone material is fragmentary or doubtful.

It is one thing, however, to recognize distinct elements in common between the Auriferous gravels and the Lamar, and another to prove the latter Miocene thereby. The former may be conceded, the latter I think not.

Lesquereux enumerates thirteen species from the Auriferous gravels which are almost identical with living species; he also cites seventeen which are evidently, but not very closely, related to living ones. Of the thirteen, four are enumerated from the Lamar; of the seventeen, not one. Of the four common to the Lamar, three are dubious, and only *Juglans leonis* (a species represented to-day by the Asiatic *J. regia*) appears to be of satisfactory standing.

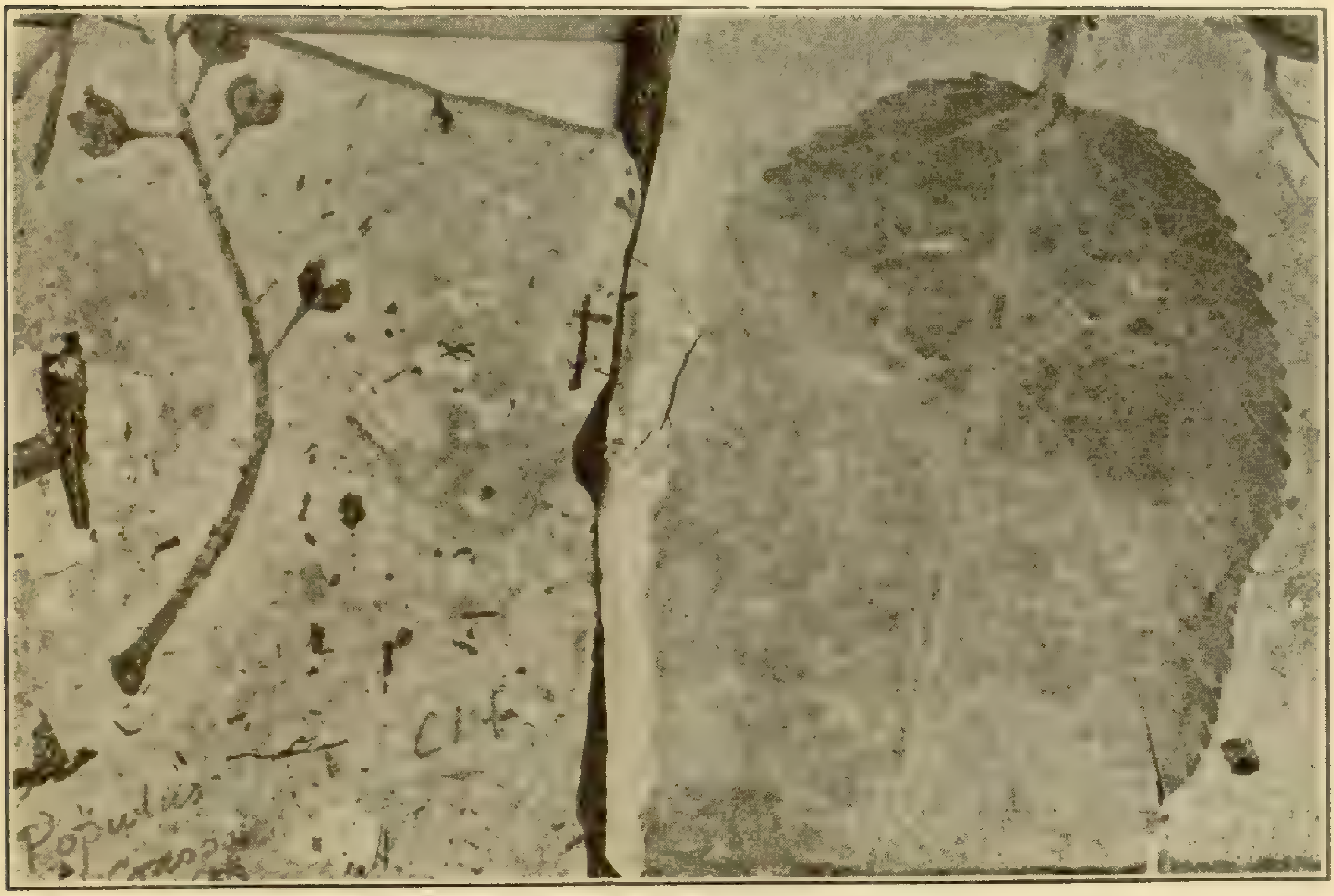


FIG. 7. **Populus crassa** (Lesquereux). Cottonwood; probably fruit of **P. lesquereuxi.**
FIG. 8. **Populus lesquereuxi** Ckll. Cottonwood.

Four species of the Auriferous gravels are said by Lesquereux to be identical with Miocene plants, but are all unsatisfactory, as follows: (1) *Fagus antipofii;* perhaps goes to the Laramie, and the Californian specimen was only half a leaf. (2) *Populus zaddachi;* supposed to go down to the Basal Eocene. (3) *Ficus tiliæfolia;*[6]

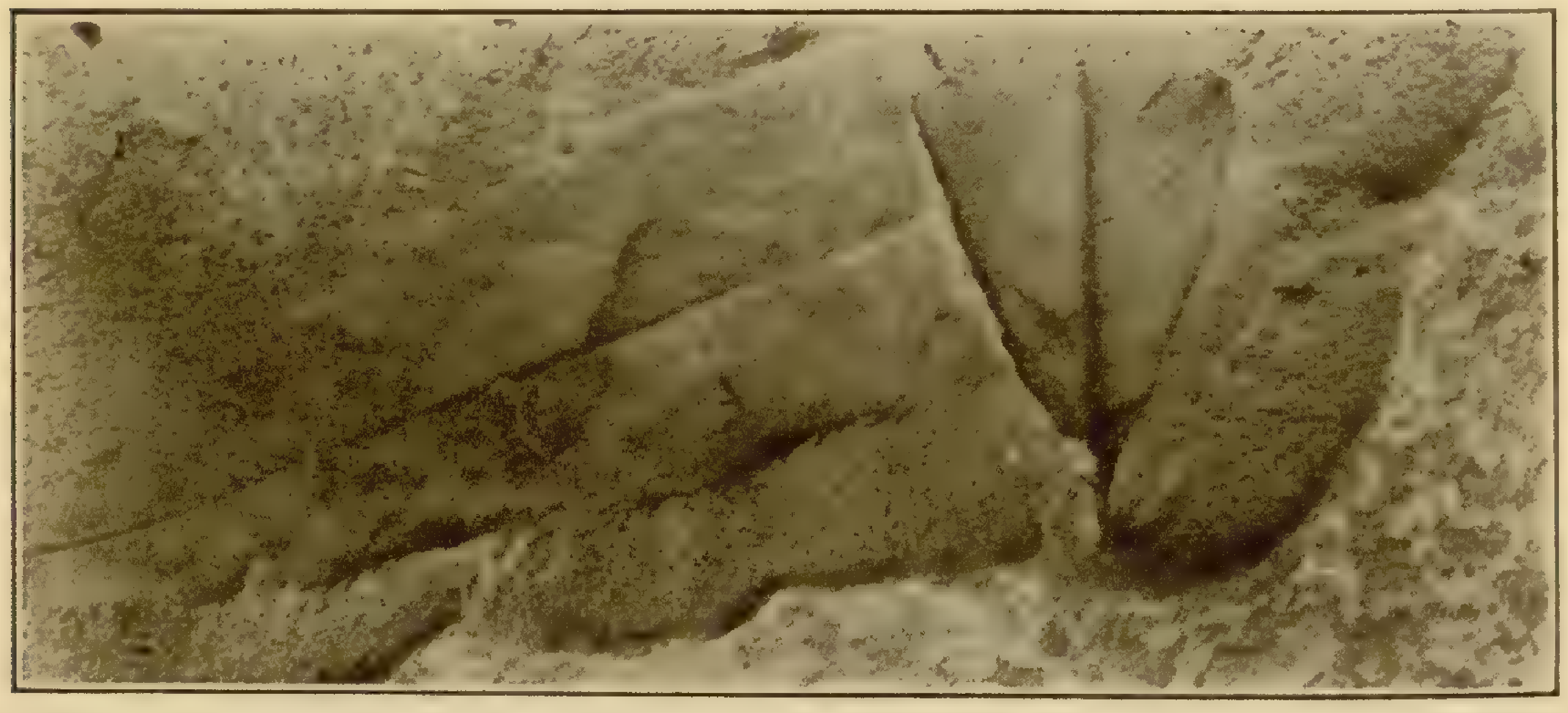


FIG. 9. **Salix ramaleyi** Ckll. Willow.

---

[6] *Ficus tiliæfolia* (A. Br.) Heer, 1856, has priority over *F. tiliæfolia* Baker, Jn. Linn. Soc. **21**: 443 (1885), from Madagascar. The latter may become **Ficus bakeriana** n. n.

said to go down to the Laramie. (4) *Aralia zaddachi;* of uncertain determination, one of the specimens was *Platanus dissecta.* None of these is found in the Lamar, but *F. antipofii* is in the Yellowstone Fort Union.

Eight other species from the Auriferous gravels are stated to be allied to Miocene species, five of these being also related to living plants. One of the five, *Juglans oregoniana,* has since proved to be from the Mascall, and not to occur in the Auriferous gravels. The other three are as follows:

> *Ficus sordida* Lx. Allied to, or perhaps identical with, *F. grœnlandica* of Greenland. A fragment referred to this has been found in the Lamar.
>
> *Ficus mensæ* n. n. (*F. microphylla* Lx., 1878, not Salzm., Mart. Fl. Braz. **4**: 93). Allied to *F. planicostata*—but this is a species of the Basal Eocene and Laramie.
>
> *Aralia whitneyi* Lx., said to be allied to an Evanston species, which would be Eocene.

It is thus apparent that the Auriferous gravels flora has no decisive Miocene affinities, but is composed of two sets of plants, one related to living forms, the other to those of the Eocene. It is known to be a mixed lot, and when I recently suggested to Dr. J. C. Merriam, of the University of California, that it might perhaps be partly Pliocene and partly Eocene, he replied that this might indeed be the case.

It is further to be remarked that Knowlton formerly regarded the Mascall flora as having affinity with that of the Auriferous gravels; but he subsequently discovered that certain of the species he had most relied on were really confined to the Mascall, and did not occur in the gravels at all. "This correlation therefore fails," he states, and the absence of relationship stands as an argument against the Miocene age of the gravels.

The conclusion seems to be legitimate that the Yellowstone Intermediate and Lamar floræ are Upper Eocene, or at least older than Miocene. Were they really Mio-

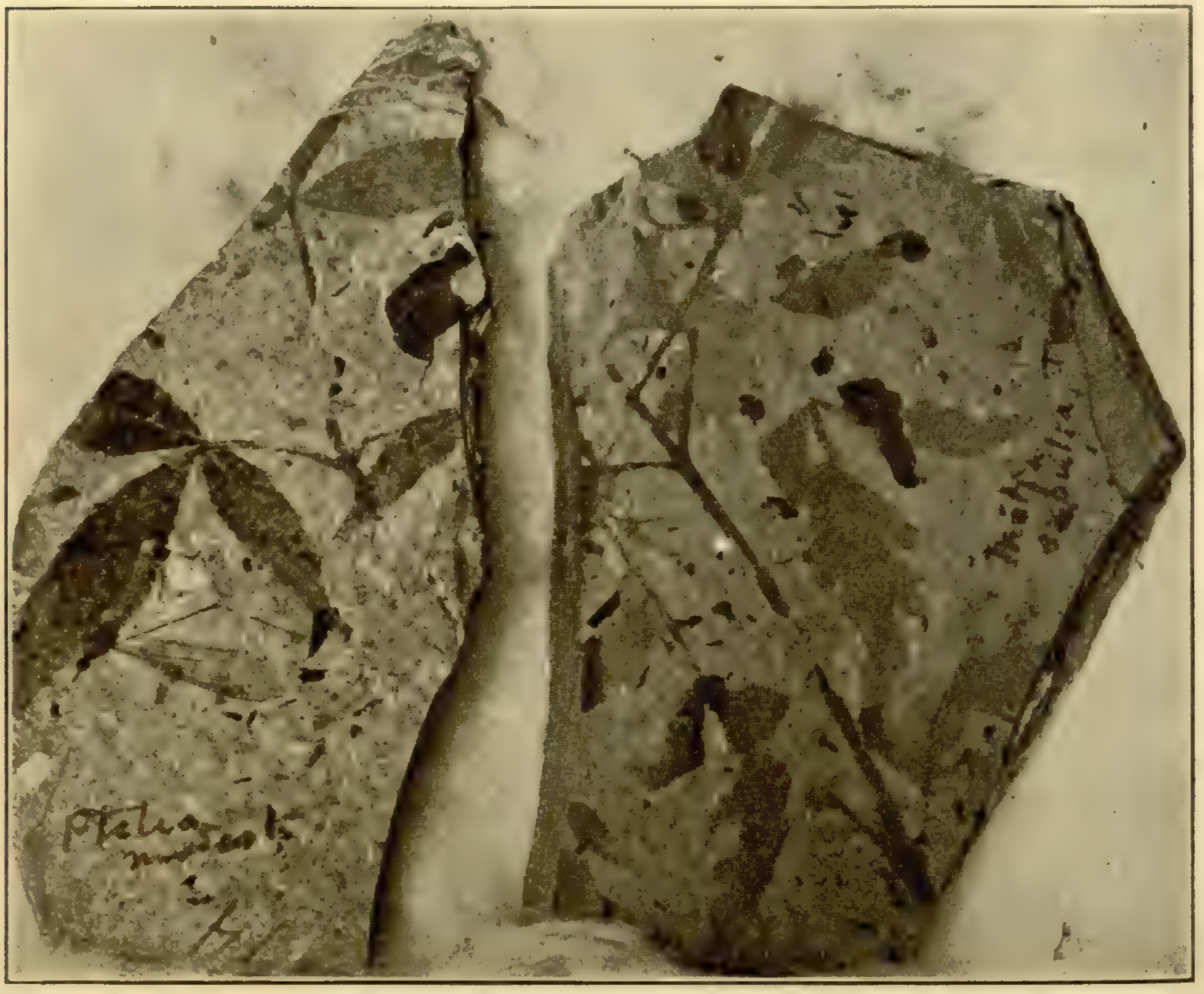


FIG. 10. *Ptelea modesta* (Lesquereux). FIG. 11. *Melia expulsa* Ckll.

cene, with so much resemblance to even the Basal Eocene, the Florissant flora, to get as far on the other side as its lack of affinity would suggest, would have to be projected somewhere into the future! If this opinion is in any degree correct, Florissant remains as the only Rocky Mountain locality for Miocene plants, so far as known.

The accompanying figures, all taken from specimens obtained at Florissant by the University of Colorado expeditions, will give a good idea of the material from that locality. Nowhere else in America are Tertiary plants so well preserved. As compared with the Eocene flora, and especially the Basal Eocene, the Florissant trees are more diverse in type, with usually smaller leaves, which are often compound. Excessively moist conditions are not indicated, though there was evidently much more moisture than at the present day. Some of the plants are even somewhat xerophytic, indicating that the higher slopes may have been relatively dry. Osborn remarks on the evidence of increasing summer droughts in the Middle Miocene. So far as the mammals are concerned, this is chiefly indicated by the plains fauna. Owing to the generally higher temperature, the air was probably moister than at present, but the moisture may have carried farther, to be precipitated on the mountains. Thus the conditions on the plains and towards the sea may have resembled those of Southern and Lower California to-day, with a comparatively damp atmosphere but little or no preciptation during a considerable part of the year. The desert fauna and flora of the southwest is a highly specialized one, which has certainly not come into existence since the Miocene, at least as regards its fundamental types; so it becomes necessary to postulate a desert region during Miocene times, and no doubt much earlier. Whether we shall ever know much about the Tertiary deserts from fossil remains is perhaps questionable, though we certainly have evidence of a semi-desert fauna, as is illustrated by the large tortoises of the Upper Miocene. The Florissant beds afford us a wonderful insight into the mountain life of the Miocene, and must have a continually increasing significance in relation to the evolution of the fauna and flora of this continent. Most unfortunately, they have as yet yielded no recognizable mammalian remains, but I am convinced that these will eventually be found. The beds are far from being exhausted, and comparatively little digging has been done at the place where fragments of a mammal were obtained—a locality which I shall be glad to describe in detail to any one who cares to go and try his luck. In the meanwhile, large collections both of plants and of insects, already obtained, remain to be investigated and reported upon, but for various reasons the work proceeds slowly.

A SUGGESTION REGARDING HEAVY AND LIGHT SEED GRAIN[1]

L. R. WALDRON

Dickinson Sub-experiment Station, Dickinson, N. Dak.

A considerable amount of work has been done by investigators of cereals, regarding the comparative value of heavy and light grains used as seed. The major portion of the experiments have been conducted with wheat, oats and barley. The problem appeared simple at the beginning, but has developed many complications.

In many cases bulk grain has been graded into various classes without determining the relative number of grains per measured quantity. Thus the experiments have been vitiated by the failure to consider the different rates of seeding, as regards the number of grains per area, which would naturally ensue. Even if allowance for seeding were made, and the number of grains per area determined as accurately as possible, it would be an excellent thing to conduct also a rate of sowing test. Such a test might throw light upon results induced by climatic conditions.

Some of the workers have made no distinction between shriveled grains and small plump grains. To eliminate the factor of shriveled grains would be virtually doing away with fanning mill methods of grading, which would seem to be necessary if we are to simplify the problem and to obviate the conflicting factors. Zavitz, of Ontario, has worked with small, hand-picked samples of grain and has evidently succeeded in overcoming the difficulties mentioned. His results, extending over a series of years, are remarkably consistent and worthy of careful study.

Despite some of the errors one can not fail to be impressed, as the literature is studied with the preponderance of evidence in favor of the large seed. The errors are as apt to tell against the heavy seed as against the light seed. In fact, where error has been most carefully eliminated, as in the experiment of Zavitz, the large seed gives the most striking positive results.

---

[1] Contribution No. III, Laboratory Experimental Plant-breeding, Cornell University.

The result, empirically derived, while of great practical importance, does not throw much light on transmission. The majority of the experimenters have paid no attention to the *plants* from which the large or small grains have come. Bolley selected large and small grains from the same heads of wheat and found that the large grains generally produced the largest yields. Lyon has stated that both large and small grains in a lot of wheat must represent both large and small spikes, and if only large grains are sown one is not necessarily selecting from the best plants.

If, according to Johannsen,[2] "In a population containing only one single type, the selection of fluctuations has no action at all," then it would make no difference, as far as transmission is concerned, if all sorts of plants were represented in the seed, so long as we are dealing with a pure line. Most American breeders, however, would prefer to select for seed the best plants from the field each year, even if working with a pure strain. This practice is doubtless based on opinion at the present time rather than on well-grounded experimental knowledge. We ought to be willing to acknowledge our ignorance of the possibility of changing the type by selecting fluctuations of close pollinated cereals. Until more and accurate data can be secured a neutral position is much the better.

CORRELATION DATA OF OATS

The writer, in securing some statistical data on oats preparatory to breeding, noticed that the data were interesting in connection with the question of light and heavy seed. Measurements were taken on 1,000 oat culms grown at Dickinson, North Dakota, under field conditions. In nearly all cases, each head-bearing culm measured rep-

---

[2] Rpt. Third Int. Conf. on Genetics, London, 1906.

X_2	—22	-20	—18	—16	—14	—12	—10	—8	—6	—4	—2	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	No. of grns.
	1	3	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	
X_1	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	
—10 150 159	1	1																															2
— 9 160 169						1				1										1													3
— 8 170 179							1				1			1				1								1						1	7
— 7 180 189										1				1	1	2	3	3	1		1	2								1			18
— 6 190 199									1		1	1	1	3	2	4	3	2	1	2	2	1	1			1		2					28
— 5 200 209	1			2		1		2	1	3	9	4	3	6	3	3	4	6	5	3	5	2		3	1	1	1	2		1	1		73
— 4 210 219		2		3	1	1	2	3	5	3	5	5	3	13	8	4	6	4	5	5	3	2	3	3		1			1				91
— 3 220 229				1	1	4	3	5	5	6	11	6	5	6	10	3	9	5	9	7	1	1		3		1			1		1		104
— 2 230 239				1	4	1	6	5	5	5	16	8	5	7	4	7	4	6	6	5	2	4	1		2		2	1					107
— 1 240 249				3	2	6	7	10	13	6	9	11	8	10	8	3	2	1	1	1	1				1	1							104
0 250 259	4		8	6	4	8	11	13	9	8	5	9	7	4	6	6	4	4	2	1			2		1								122
1 260 269		4	1	1	4	6	10	6	8	4	6	5	5	4	1	3	4		1		2												75
2 270 279	1	3	2	5	9	7	6	9	9	8	3	5	1	5	1	1		1	2														78
3 280 289		6	3	6	6	5	7	7	3	7	2		2	1																			55
4 290 299			8	3	5	4	5	6	1	1	1	1	1	1		1																	33
5 300 309	3	4	9	12	3	4	5	3	1	1	2			2																			46
6 310 319	1	4	5	4	4	1	1	1																									21
7 320 329	3			3	3	1					1																						11
8 330 339		2	1	2	1	1					1																						8
9 340 349			2	1																													3
10 350 359	2	1	2	3																													8
11 360 369																																	0
12 370 379	2																																2
13 380 389		1																															1
Weight deci-mg.	18	28	36	56	47	51	61	70	61	54	73	58	41	64	44	37	39	33	33	25	17	12	7	9	5	6	3	5	2	2	2	1	1000

Fig. 1. Correlation in oats.[3] Average weight of grains subject, number of grains per head relative. Coefficient of correlation, — 0.595 ± 0.013.

X_2	—10	—9	—8	—7	—6	—5	—4	—3	—2	—1	0	1	2	3	4	5	6	7	8	9	Head cm
X_1	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
—10 150 159	1							1													2
— 9 160 169								1					1					1			3
— 8 170 179										1	1			2	2				1		7
— 7 180 189										1		3	4	3	4	1	2				18
— 6 190 199										2	3	5	11	1	3	2		1			28
— 5 200 209						2		2	2	3	11	14	13	10	8	3	4	1			73
— 4 210 219				1	1		1	1	4	8	10	15	18	18	11	3					
— 3 220 229								2	5	15	17	16	24	11	6	7		1			104
— 2 230 239							2	3	10	14	18	17	17	14	7	3	2				107
— 1 240 249					1	1	4	7	8	12	21	18	16	10	4	1				1	104
0 250 259	1		2	1	4	2	4	10	20	21	17	9	17	7	5	1	1				122
1 260 269					2		3	6	12	14	13	11	7	3	3	1					75
2 270 279			1	1	2	2	3	12	8	13	7	13	8	5	2	1					78
3 280 289					2		9	5	7	10	10	4	4		3	1					55
4 290 299						1	1	5	8	11	2	2	2		1						33
5 300 309					1	5	9	8	7	7	6	2			1						46
6 310 319				2		1	4	7	2	3		1				1					21
7 320 329				2	1		1	3	2	2											11
8 330 339						1	1	3	1		1			1							8
9 340 349						1	1	1													3
10 350 359				1	3		2	1	1												8
11 360 369																					0
12 370 379					2																2
13 380 389						1															1
Weight deci-mg.	2		3	8	19	17	45	78	97	137	137	130	142	91	54	25	9	4	1	1	1000

Fig. 2. Correlation in oats. Average weight of grains subject, length of head relative. Coefficient of correlation, — 0.511 ± 0.015.

---

[3] The weights of the grains in the first five figures are expressed in decimilligrams. The lengths are expressed in centimeters. In Fig. 6 the weight is expressed in milligrams and the volume in cubic millimeters.

resented an entire plant. The variety is well defined morphologically, but evidently contains various races or biotypes.

Among other data secured was the height of culm, the length of head, the number of grains per head and the average weight of kernel. The various measurements were correlated and the results prove very interesting.

Fig. 1 shows the correlation existing between the average weight of kernel as subject and the number of grains per head as relative. A strong negative correlation is noticed, amounting to very nearly 60 per cent. In other words, the greater the number of grains per head, or, in reality, the larger the head as regards grain, the less the average weight per kernel.

The mean of the number of grains per head, of the population studied, is 22.098 and the mean weight per kernel is 24.913 mg.

The regression coefficient of the number of grains relative to the average weight of grain is — 1.98. In other words, if we should select grains for planting that weigh, for instance, 30 mg. and above, they would on the whole be selected from heads containing only about 12 or 13 grains, which represent heads considerably below the mean. There would doubtless be an occasional grain from heads above the mean, but such grains would be uncommon and the increasingly larger heads would be more and more sparsely represented in the grain selected for planting.

Fig. 2 shows the correlation existing between the average weight of kernel as subject and the length of head as relative. As the number of grains is quite dependent upon the length of head we should expect to find a correlation existing between the two, somewhat similar, as is shown in Fig. 1. The actual correlation is negative and amounts to 51 per cent. The mean length of the head is 13.583 cm.

The regression coefficient of the length of the head relative to the average weight of grains is — 0.379. That is, if we should select grains for planting that weigh, for instance, 30 mg. and above, they would in general be

X_2	−36	−34	−32	−30	−28	−26	−24	−22	−20	−18	−16	−14	−12	−10	−8	−6	−4	−2	0	2	4	6	8	10	12	14	16	18	20	Height cm.
	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	
	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	70	72	74	76	78	80	82	84	
X_1																														
−10 150 159	1										1																			2
− 9 160 169															1	1									1					3
− 8 170 179														1		1		1	1	1				1	1					7
− 7 180 189																		3	2	5	6		2							18
− 6 190 199														2	1	2	1		3	1	6	8	1	3						28
− 5 200 209						1					2	2		1		4	5	2	11	11	5	10	7	7	1	2	2			73
− 4 210 219						1				1		2	1	3	4	5	5	5	13	11	9	16	6	4	3		2			91
− 3 220 229												1	3		2	13	9	8	9	13	10	8	8	10	4	3	3			104
− 2 230 239										1	1	1	2	3	4	7	9	11	10	14	9	9	13	3	4	4	1	1		107
− 1 240 249										1	2	4	1	1	7	7	15	13	8	12	16	8	3	1	2	1	2			104
0 250 259	2					1		1	2	4	1	5	9	10	4	6	10	10	9	7	9	16	9	4	3					122
1 260 269									1		3	3	1	5	7	13	6	5	3	1	8	8	5	2	3	1				75
2 270 279				1	1	1	1			2	1	5	5	5	5	6	4	12	4	6	10	2	3	2		1			1	78
3 280 289						2		1	1	1	2	4	2	5	12	3	2	5	5	5	1	1	1	1				1		55
4 290 299								2		1			4	3	3	2	5	3	2		2	2				3	1			33
5 300 309						1	1	2	1	3	3	6	5	4	5	4	1	2	3	1	1	2		1						46
6 310 319								1	2		3	2	4	3	3	1			1		1									21
7 320 329					1			1		1		2	1	1	1		2	1												11
8 330 339											1	3			2			1				1								8
9 340 349									1		1					1														3
10 350 359						1	1				1	1	3					1												8
11 360 369																														0
12 370 379												1	1																	2
13 380 389												1																		1
Weight deci-mg.	3	0	0	1	2	8	3	8	8	15	22	43	42	47	61	76	74	83	84	88	93	91	58	39	22	15	11	2	1	1000

FIG. 3. Correlation in oats. Average weight of grains subject, length of culm relative. Coefficient of correlation, — 0.404 ± 0.017.

X_2	−14	−12	−10	−8	−6	−4	−2	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	No. of grns.
	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	
	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	
X_1																														
−11 80 89															1															1
−10 90 99								3																						3
− 9 100 109						1						1													1					3
− 8 110 119						1		1						1																3
− 7 120 129		1	1			1					1	1			1															6
− 6 130 139				1	1		1	1		2	3	2	1				1													13
− 5 140 149						2	1		3	1	1		1																1	10
− 4 150 159				1	1	1	2	1	3	2	2	1	1	2																17
− 3 160 169				2	1	1	5	3	9	1	2	1						1		1		1								28
− 2 170 179		1			5	3	11	3	1	4	3	4	2	2	2															41
− 1 180 189			1	1		4	4	5	9	5	5	3	6	2	3			1												49
0 190 199				1	4	2	5	9	6	4	9	3	4	2	1	1				1										52
1 200 209		1	1	2	3	1	2	8	5	7	4	3		1	1		1													40
2 210 219					1	1	6	3	4	3		2	4																	24
3 220 229		1		1		1	4	3	1	3	4		5	1			1													25
4 230 239					1	2	3	3	3	2	1		1																	16
5 240 249					1			1		1	1	1					1													6
6 250 259		2				1	2	1				1																		7
7 260 269						1							1																	2
8 270 279												1	1																	2
9 280 289	1	1																												2
10 290 299		1																												1
11 300 309							1																							1
12 310 319							1																							1
13 320 329																														0
14 330 339																														0
15 340 349																														0
16 350 359																														0
17 360 369																														0
18 370 379																														0
19 380 389																														0
20 390 399														1																1
Weight deci-mg.	1	8	3	9	18	23	48	45	44	35	36	24	27	12	9	1	4	2	0	2	0	1	0	0	1	0	0	0	1	354

FIG. 4. Correlation in winter wheat. Average weight of grains subject, average number of grains per head relative. Coefficient of correlation, — 0.115 ± 0.031.

selected from heads in the neighborhood of 11.5 cm. long. We should have to select the shorter heads in order to secure the larger grains.

Fig. 3 shows the correlation existing between the average weight of kernel as subject, and the total height of culm, including the head, as relative. The correlation is still negative and amounts to 40 per cent. The mean length of the culm is 61.74 cm.

The regression coefficient of the length of the culm relative to the average weight of grain is — 0.987. As in the last example, the selection of grains weighing 30 mg. and above would imply that they had come from culms about 56 cm. long, or about 5 cm. below the mean.

As a summary, plants with shorter culms, shorter heads, and with a smaller number of grains, bear on the whole grains of a greater weight. The opposite of course is equally true.

If the data had been taken of a pure strain of oats, of the variety studied—of a number of plants that had come within a few generations from a single mother plant—then the correlations might have varied slightly from those given. If data were accessible of another variety, then we might suspect even greater deviation from the figures given. Variation in the same variety from year to year may be expected. However, there is nothing to lead us to believe, from an *a priori* standpoint, that the data given would be essentially changed.

If data were taken on oat plants grown in hills, then we might get less decided negative correlations than those given where the plants were grown under field conditions. The variability of the number of grains, the height of plant and the length of head might be less, while the variability of the average weight of grain might not be much different.

The following table shows the coefficients of variability expressed in per cent. of the various factors that have been discussed.

The factor of the number of grains is evidently the much more variable one and perhaps under hill condi-

		X_2	−34	−32	−30	−28	−26	−24	−22	−20	−18	−16	−14	−12	−10	−8	−6	−4	−2	0	2	4	6	8	10	12	14	16	18	20	22	24	26	Height cm.
			37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	
			38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	70	72	74	76	78	80	82	84	86	88	90	92	94	96	98	
X_1																																		
−11	80	89																																1
−10	90	99																				1		1			1							3
−9	100	109							1									2																3
−8	110	119										1								1	1													3
−7	120	129					1	1					1			1			1		1													6
−6	130	139	1				1				1					1	2	2	4			1												13
−5	140	149							2			1		1			1	4										1						10
−4	150	159					1					1	1	2		1	1			2		4		1	1			1	1					17
−3	160	169							1	1	1	1	2	1			3	1	1	2	1	1	4	3	1		1		2	1				28
−2	170	179				1				1	1	4	2			3		3	5	1	5	4	3	3	2	1		1				1		41
−1	180	189						1	2		1	1	1	3			3	2	3		4	6	3	5	5	1	3	1	1	3				49
0	190	199		1				1			1	3	1	3	4		6	3	2		2	1	6	2	5	3	3	1	1	1		1	1	52
1	200	209							1	2	2			3	3		2	1	1	2	4	5	4	1	1	2	1	1	2	1		1		40
2	210	219			1								1					1	2	3	2	2	1		2	1	2	1	4			1		24
3	220	229					1							1	2	2		2	2		3	2	3	2		1	1	1	1	1				25
4	230	239												1			3			1		1	1	1		1	2	2	1	1		1		16
5	240	249										1		1			1						1	1					1					6
6	250	259								2							1								1		1	1				1		7
7	260	269																			1											1		2
8	270	279																	1					1										2
9	280	289					1	1																										2
10	290	299							1																									1
11	300	309																									1							1
12	310	319																									1							1
13	320	329																																0
14	330	339																																0
15	340	349																																0
16	350	359																																0
17	360	369																																0
18	370	379																																0
19	380	389																																0
20	390	399																1																1
Weight deci-mg.			1	1	1	1	5	4	8	6	7	13	9	16	9	8	23	22	22	12	24	28	26	22	18	10	17	11	14	8	0	7	1	354

Fig. 5. Correlation in winter wheat. Average weight of grains subject, average length of culm relative. Coefficient of correlation, 0.16 ± 0.034.

	X_2	−6	−5	−4	−3	−2	−1	0	1	2	3	4	5	6	7	8	Vol. cu. mm.
		14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	
X_1																	
−8	19		1														1
−7	20	1	3	2													6
−6	21		1	2							1						4
−5	22			4	2												6
−4	23			2	6	1					1						10
−3	24				4	8											12
−2	25				2	12	10										24
−1	26					4	13	3									20
0	27						7	16									23
1	28						1	12	5	1						1	20
2	29							1	13	4							18
3	30							1	7	8	1						17
4	31									6	2						8
5	32									1	4	4					9
6	33										2	3					5
7	34											1	1				2
8	35												1	1			2
Weight mg.		1	5	10	14	25	31	33	25	20	11	8	2	1	0	1	187

Fig. 6. Correlation in winter wheat. Average weight of grains subject, average volume of grains relative. Coefficient of correlation, 0.896 ± 0.009.

tions it would be somewhat reduced, though this is only problematical.

Factor.	Coefficient of Variability.
Number of grains	54.5 ± 2.33
Average weight of grains	14.5 ± 0.48
Length of head	19.7 ± 0.68
Length of culm	14.2 ± 0.47

Since the above was written it has been found that the small oat heads bear a somewhat larger percentage of single grains than the large heads. If this factor be considered, the negative correlations would be somewhat decreased but probably not materially.

CORRELATION DATA OF WHEAT

In looking over the literature some unreduced winter wheat data were found in Bulletin 78 of the Bureau of Plant Industry by Dr. T. L. Lyon. A portion of this data was thrown on to correlation tables and is given herewith.

Fig. 4 shows the correlation existing between the average weight of kernel as subject and the average number of grains per head as relative. Both the weight and number are averages for the entire plant. The figures are thus not quite comparable to those given for the oat plants, but are doubtless nearly so. Data for only 354 individual plants are given, but this number of plants represents a considerably larger number of culms. The correlation is negative and is a little over 11 per cent. The regression of the average number of grains relative to the average weight of grains is much diminished and a selection of seed of either very high or of very low weight would not indicate that the seed was from plants located any appreciable distance from the mean, as far as average number of grains is concerned.

Fig. 5 shows the correlation existing in winter wheat between the average weight of kernel as subject and the average height of culm as relative. As in the previous case, data for only 354 individuals are given. Instead of a negative correlation, as in all previous cases, we have here a positive correlation, amounting to 16 per cent. This is a weak correlation. The regression of the average height of culms is very slight. Selection of any particular weight of seed would not imply that any particular heights of plants were involved.

It is interesting to note that the correlations given of winter wheat hold about the same relations to each other as do the corresponding correlations of the oats.

Relation of Size to Volume of Grain

But little accurate data on this point are available. We should expect to find a close correlation. The data given in Fig. 6 are taken from Bulletin No. 78 mentioned previously. It is seen that there is an almost perfect correlation existing between the average weight of kernel and the average volume per kernel. The three outstanding individuals suggest errors rather than extreme variations.

Summary

If oat populations in general show constants similar to those given, then the experimenter selecting the large grains is not selecting from what is commonly considered the best plants, and *vice versa*. If the plants from large grains produce a better yield, then they must do so by virtue of the increased vigor of the embryo and the increased amount of food supply. If we consider that the size and yield of the mother plant have an influence upon the size and yield of the daughter plants, then we must consider that this influence is decidedly less than the influence exerted by the size of the seed. If the size and yield of the mother plant have no effect upon the offspring, then we might expect the yields from different weights of seed to be somewhat in proportion to the weights of seed.

Despite all that has been written on the foregoing points we have very little accurate knowledge pertaining thereto, especially relative to the influence of selection upon the close pollinated cereals.

NOTES AND LITERATURE

MAMMALOGY

Nelson's Monograph of the North American Leporidæ.—Mammalogists owe a debt of gratitude to Mr. E. W. Nelson for his recent monographic revision of the hares and rabbits of North America,[1] the first revision of the group as a whole since the publication of Allen's monograph of this group in 1877. Mr. Nelson, in addition to abundant material, has brought to his task an intimate knowledge of these animals in life, and of the environments to which the different groups of species are subjected, through his many years' experience as an explorer and collector, covering a wide area, embracing Arctic Alaska, the arid southwestern United States, Lower California, and the whole of Mexico, including the tropical coast lands as well as the plateau region. The monograph is based on the careful study of nearly 6,000 specimens, all of the material contained in the principal museums of America having been examined. The number of species and subspecies recognized is 97, of which 93 are contained in the collections of the United States National Museum. This is an increase of nearly 80 over the number known in 1877.

The introduction (pp. 9–61) deals with the economic relations of the American rabbits to agriculture; the use of the names rabbit and hare; the condition of the young at birth; the distribution of the genera and species; their habits and diseases; their color patterns, molts and seasonal changes of color; sexual, individual and geographic variation; their classification, and keys to the species and subspecies.

Points of general interest are the destructiveness of these animals to vegetation, through injury to young trees, both in orchards and newly planted forests; and their food value, which, as is well known, is considerable, millions of rabbits being sold in our markets each winter.

The names hare and rabbit were originally used in a specific sense to designate the two long-known European species; later their use became greatly broadened and their application more or less interchangeable, with different restrictions by different authorities and in different countries. Mr. Nelson would confine the use of the term hare, so far as American species are concerned, to the restricted genus Lepus (including the varying and Arctic hares and the jack rabbits), and employ the term rabbit for the "cotton-tails" or smaller brush rabbits and swamp rabbits (genus Sylvilagus and allied forms). The hares are, generally speaking, larger than the rabbits, live mostly in "forms," and bring forth young with open eyes and well-clothed with hair; many of the rabbits are known to bring forth their young naked and blind; while some of them burrow, others live in forms, like the true hares.

---

[1] "The Rabbits of North America," by E. W. Nelson, chief field naturalist, Biological Survey. Prepared under the direction of Dr. C. Hart Merriam, Chief of Bureau of Biological Survey. North American Fauna, No. 29, August 31, 1909. 8vo, pp. 1–314, pl. i–xiii, and 19 text figures.

Formerly all the species of Leporidæ were referred to the single genus Lepus, but later, mainly within the last decade, several genera have been recognized by the leading authorities on the group, together with a number of subgenera. Mr. Nelson arranges the North American species in four genera—Lepus, Sylvilagus, Brachylagus and Romerolagus. The last two are monotypic with very restricted ranges; the rest of the species are assigned to Lepus (with two subgenera, Lepus = Arctic and varying hares, and Macrotolagus = "jack rabbits") and Sylvilagus (also with two subgenera, Sylvilagus = "cotton-tails" or brush rabbits) and Tapeti (swamp rabbits. The latter includes most of the species of Central and South America).

The hares of the subgenus Lepus (the Arctic and varying hares) have a double molt, being brown in summer and white in winter, while the other species are believed to molt, for the most part at least, only once (in fall), and the only seasonal change of color is due to the fading and abrasion of the long-worn coat. Formerly it was supposed that the white winter coat of all the northern hares was due to a change of color in the hair itself of the summer coat. On this point Mr. Nelson says:

> The change in color from the white winter pelage of northern species to the dark summer coat, or *vice versa*, is accomplished so gradually that at certain stages it appears like a change in the color of the hairs instead of a molt, as was definitely proved by Doctor Allen in his paper on the changes of pelage of the varying hare.[2]

This supposed change of color in the hairs, he further says,

---

[2] *Bull. Am. Mus. Nat. Hist.*, VI, pp. 107–128, May 7, 1894.

"may be readily disproved by a careful examination of a few molting specimens." It is also now well known that the white winter coat of the ermines and weasels, and of such species of lemmings as turn white in winter, is due to molt and not to a blanching of the hairs of the summer coat. In other words, seasonal change of color in mammals, as well as in birds, is due entirely to molt. In the case of the hares and weasels, the change to white in winter is only partial at the southern border of the ranges of species that further north become wholly white in winter, while the most northern forms of the Arctic hare group remain practically white in summer, as in northern Greenland and northern Ellesmere Land. The time of molt also varies with the character of the season. As has long been known, an early spring or fall brings on the molt a month or more earlier than a later one, and hence a change of color in such species as have a white winter livery is correspondingly later.

Mr. Nelson confirms the statements of previous writers that the pelage in mammals is in other ways subject to modification by the environment, as through variation in its length and density in accordance with the severity of the climate. In discussing the effect of environment, he also confirms the experience of other mammalogists, and of ornithologists and herpetologists as well, that "like climatic conditions often produce the same or closely similar colors in dissimilar species," and also parallel modifications in other features, including cranial details of structure.

> These fluctuations are somewhat wavelike in character and rise to central points of extreme development and then sink away to intermediate borders beyond which new waves arise. When the waves of differentiation are pronounced they mark recognizable geographic races. . . . In the case of wide-ranging subspecies such fluctuations are frequent, especially where the areas occupied are diversified by mountains. These fluctuations, which are sometimes extremely local, mark, of course, potential subspecies. Some are fairly well characterized and eventually may be named, while others are too slight to be formally recognized by name, but well serve to illustrate the plastic condition of the species. The transition from one subspecies to another takes place abruptly or gradually in exact accord with the changes of environment which produce them. . . .

As is well known, many mammals are subject to periodic destruction by disease. This is especially marked among rodents.

such as voles, ground-squirrels and rabbits, and their reduction or increase in numbers, as the case may be, powerfully affects the welfare of such species of mammals and birds as prey upon them. In the case of rabbits, destruction by epidemics is periodical, occurring apparently about once in seven years, although exact data are wanting as to the regularity or frequency of these epidemics, or their exact nature. They are at times so severe that only a few individuals are left to perpetuate the species. They are also followed, there is some reason to believe, by an increased birthrate by which the stock is rapidly replenished. This periodic destruction is considered by Mr. Nelson in relation to the apparent opportunity thus afforded for the origination, through isolation, of many strongly characterized forms, but he fails to find evidence that this is an evolutionary force of much importance. The *Lepus americanus* group, occupying the vast wooded area from Nova Scotia to western Alaska, which has been subjected to numberless recurring periods of extreme abundance and extreme scarcity, presents only a few, and not strongly, differentiated subspecies, owing, it is believed, to the leveling influence of similarity of climate.

In illustration, however, of the effects of complete isolation under similar climatic conditions, the black jack rabbit of the island of Espiritu Santo is cited. This small island lies off La Paz Bay, Lower California, only four miles from the mainland, from which it is separated by a channel having in its shallower parts only four to five fathoms of water. The island was doubtless formerly a part of the mainland, and has still the same character of vegetation and climate. The adjacent mainland is occupied by a pale form of the *Lepus californicus* group, the island by a form essentially the same in size and cranial characters, but so dark in color as to be commonly referred to as the ''black'' jack rabbit. The intensification of color, making it ''extraordinarily conspicuous,'' has not been ''protective,'' nor yet has it proved a detriment, presumably from the fact that no predatory mammal or large bird of prey shares its habitat.

Coming now to the systematic portion of the monograph, it may be noted that the genera and subgenera here recognized are very satisfactorily characterized, and the keys to the species and subspecies are carefully elaborated, occupying ten pages for the 97 forms recognized. These, in the systematic part of the monograph, are treated very fully in respect to their distinctive characters, ranges and relationships. There is, however, very little on the historical side of the subject beyond a briefly annotated bibliography of sixty-six titles (pp. 282–287), prefaced by a page and a half of historical résumé. The citations under the species relate almost wholly to synonyms, which in this group of American mammals are fortunately exceptionally few. There is little to indicate the point of view of previous writers, or their manner of treatment as regards forms recognized and their allocation. The correlation, from the author's standpoint, of work previously done is an essential feature of a monographic treatise; and this can be fairly shown in tables of reference,[3] with such slight additional comment as may seem necessary. This defect in the present case is doubtless a feature of environment, due to limitations already referred to in another connection.[4] Yet it seems strange to find no reference under the genus Romerolagus to the discussion of the structure and affinities of this interesting type by previous authors, as Lyon, Major and Herrara, nor to the alleged earlier competitive name for the species, namely *Lepus diazi* Ferrari Perez (1893).

As already intimated, the systematic treatment is in general excellent. The species is first considered as a whole; its subspecific components are passed in review, their ranges shown graphically on a map, and a table gives the average measurements, external and cranial, of five specimens of each form, the same external measurements being repeated later in their proper connection in the text. This number, however, is too few to be satisfactory, and extremes of variation are not indicated. Under the subspecies the geographic range is first indicated, followed by a paragraph of "general characters," and very full descriptions of the coloration, seasonal variations, cranial distinctions, and such "remarks" as circumstances may require. In view of the material studied by the author, and his standing as an investigator, criticism of details would be out of place unless based on equal opportunities. Mr. Nelson, however, has given a decidedly new aspect to the nomenclature of the group, through the revival of certain previously unidentified names, the merging of the *texianus* group of former authors with the *californicus* group, of the *arizonæ* group with the *audu-*

---

[3] Note, for example, the synonymies in Ridgway's "Birds of North and Middle America."

[4] AMERICAN NATURALIST, Vol. XLIII, October, 1909, p. 639.

boni group, the reduction to subspecies of numerous forms previously recognized as species, and the raising to specific rank of forms formerly treated as subspecies.

The only new form appears to be a subspecies *littoralis* of *Lepus aquaticus* Bachman, through the assignment of a type locality for *aquaticus*. As Mr. Nelson says, there "was no definite type," and the species was described "from specimens obtained in western Alabama by Dr. J. M. Lee. . . . No definite type locality is mentioned, but the context appears to indicate that these specimens came from western Alabama, which may be considered the type region." He further states that "the types do not appear to have been preserved," and were thus unavailable as an aid in settling the type locality. In the original account of this species Dr. Bachman said that he did not know of its existence "to the east or north of the State of Alabama," but that "it is numerous in all the swamps of the western parts of that state, is still more abundant in the State of Mississippi and the *lower parts*[5] of Louisiana, and is frequently brought by the Indians to the market of New Orleans." If Mr. Nelson had been the first to split the *Lepus aquaticus* group into a Gulf coast form and an interior form his course would be justifiable, but this division was made long before, when the *Lepus aquaticus attwateri* was separated on the basis of comparison of specimens from the vicinity of San Antonio, Texas, with a series from the vicinity of New Orleans. He recognizes only the same two forms, so that his *littoralis* is properly a synonym of *Lepus aquaticus aquaticus*, with the name of the interior form still *Lepus aquaticus attwateri*. Were it conclusively known that the type locality of *aquaticus* was within the range of the interior form, he would be fully justified in his present ruling, but in view of the fact that it is at best conjectural, and that the same division of the species he now makes had been made before, thus in effect restricting the name *aquaticus* to the Gulf coast form, his action in the case seems at least open to reasonable objection.

The illustrations comprise twelve excellent plates (from photographs) of skulls of the different leading types of North American hares and rabbits, a plate (from a wash drawing) of "directive coloration in *Lepus callotis*," and nineteen text figures, sixteen of which are distribution maps, and three illustrate osteological characters in the genera Lepus and Sylvilagus.

---

[5] Not italicized in the original.

The "directive coloration" plate shows two specimens of a Mexican species of jack rabbit, which has white sides and a dark buffy mantle covering the back. One figure shows the mantle in its usual position, the other with the mantle "shifted to the opposite side and the whitish area of the side drawn up nearly or quite to the dorsal line," the animal being then in the act of "signalling." This extraordinary feat is described at length on page 115, where it is said that "By means of muscles the skin of either side can be drawn over the back at will." Mr. Nelson further states that on one occasion one of these rabbits observed by him kept the "white area in the same position until it had traveled 50 or 60 yards, when the colors slowly resumed their normal positions."

Despite the slight criticisms we have felt called upon to make, Mr. Nelson's "The Rabbits of North America" marks an era in the history of the group, and is so comprehensive and so well done that it must long remain the basis for future work, to be corrected doubtless in many minor details as new material is received, but nevertheless a boon to all workers in North American mammalogy.

J. A. ALLEN.

AMERICAN MUSEUM OF NATURAL HISTORY.

NEUROLOGY

Edinger's "Vorlesungen über den Bau der nervösen Centralorgane" made its first appearance as a small volume in 1885. Its directness and lucidity gained for it at once a deserved popularity and a growing demand justified the numerous editions under which it subsequently appeared. In its latest form, the seventh edition, the work consists of two volumes, either of which is about twice the size of the original edition. This considerable expansion has taken the work away from the circle of readers, mostly medical students and physicians, for whom the earlier editions were intended. It is therefore natural that an effort should be made to return to the earlier form and this effort has found its realization in the present "Introduction."[1] This volume, which contains a little less than two hundred pages, is a summary of the larger work, but with the emphasis laid on the human central nervous organs. The presentation has the great advantage of beginning with the consideration of the spinal cord, the more primitive part of the central nervous system, and then proceeding to the more specialized part, the brain, instead of dealing with these subjects in the reverse order as in the early editions of the "Lectures." The condensation has been most admirably done, and, as a work that is intended to state briefly those matters that are best established for the structure of the central nervous organs in man, it is a masterpiece. The regrets that one may have about the volume are chiefly because of omissions, but condensation implies omissions and it is hard to imagine under the circumstances a better selection of materials. In one respect the general presentation might perhaps have been improved. It is strange that Dr. Edinger, who accepts the neurone theory so completely, should have abandoned this method of presentation in dealing with the brain, though he adopts it in his account of the cord. Possibly, however, the greater uncertainty of resolving the brain from the standpoint of the neurone as compared with the cord, is a justification for this difference of treatment. In illustration and typography the volume is on as high a level as in subject matter.

---

[1] Edinger, L., "Einführung in die Lehre vom Bau und den Verrichtungen des Nervenssystems." Leipzig, F. C. W. Vogel, 190 pp., 161 figures, 1 plate, 1909.

G. H. Parker.

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE JULY NUMBER

Selection Index Numbers and their Use in Breeding. Dr. RAYMOND PEARL and FRANK M. SURFACE.

A Contribution to the Theory of Orthogenesis. Dr. ALEXANDER G. RUTHVEN.

The "Presence and Absence" Hypothesis. Dr. GEORGE HARRISON SHULL.

Present Problems in Plant Ecology: Vegetation and Altitude. Professor CHARLES H. SHAW.

Shorter Articles and Correspondence: Pleistocene Swamp Deposits in Virginia. Dr. EDWARD W. BERRY.

Notes and Literature: *Heredity*—A Case of Non-Mendelian Heredity. Dr. W. J. SPILLMAN.

CONTENTS OF THE AUGUST NUMBER

The New Flora of Krakatau. Professor DOUGLAS HOUGHTON CAMPBELL.

A Male Crayfish with Some Female Organs. Professor E. A. ANDREWS.

Present Problems in Plant Ecology:

Problems of Local Distribution on Arid Regions. Professor VOLNEY M. SPAULDING.

The Relation of the Climatic Factors to Vegetation. Professor EDGAR N. TRANSEAU.

Notes and Literature: Recent Experiments on the Inheritance of Coat Colors in Mice, Professor T. H. MORGAN. Some Experiments in Breeding Slugs. Professor T. D. A. COCKERELL.

CONTENTS OF SEPTEMBER NUMBER

On an Early Tertiary Land-connection between North and South America. Dr. R. F. SCHARF.

Notes on the Relations of the Molluscan Fauna of the Peruvian Zoological Province. Dr. WILLIAM HEALEY DALL.

Remarkable Development of Starfishes on the Northwest American Coast; Hybridism; Multiplicity of Rays; Teratology; Problems in Evolution; Geographical Distribution: Professor A. E. VERRILL.

Shorter Articles and Correspondence: Is there a Selective Elimination of Ovaries in the Fruiting of the Leguminosæ: Dr. R. HARRIS.

Notes and Literature: *Ichthyology*—Ichthyological Notes, President DAVID STARR JORDAN. *Parasitology*—Professor H. B. WARD. *Plant Cytology*—The Permanence of Chromosomes in Plant Cells, Dr. BRADLEY M. DAVIS.

CONTENTS OF THE OCTOBER NUMBER

The Non-muscular Articulations of Crinoids. AUSTIN HOBART CLARK.

On Some Dinichthyid Armor Plates from the Marcellus Shale. BURNETT SMITH.

Are Species Realities or Concepts only. Professor J. H. POWERS.

Shorter Articles and Discussion: A Light Weight, Portable Outfit for the Study and Transportation of Ants. EDITH N. BUCKINGHAM. Comparison of Cænolestes with Polyprotodonta and Diprotodonta. PAULINE H. DEDERER.

Notes and Literature: *Comparative Psycholoy* — Bohn's "The Birth of Intelligence": Professor H. S. JENNINGS. *Mammalogy*—Osgood's Revision of the Mice of the Genus Peromyscus, Dr. J. A. ALLEN, LEO ERRARA, Professor CHARLES E. BESSEY.

CONTENTS OF THE NOVEMBER NUMBER

The American Toad (Bufo lentiginosus americanus LeConte). NEWTON MILLER.

Notes on the Behavior of the Domestic Fowl. PHILIP B. HADLEY.

Vitality of Pine Seeds and the Delayed Opening of Cones. Professor W. C. COKER.

The Affinities of the Echinoidea. AUSTIN HOBART CLARK.

The Early Breeding Habits of Amblystoma punctatum

Notes and Literature: *Marine Biology*—Papers from the Tortugas Laboratory, Professor WILLIAM E. RITTER. *Experimental Evolution* — Inheritance of Color in Pigeons, B. B. HORTON.

CONTENTS OF THE DECEMBER NUMBER

The Cuticula and Subcuticula of the Trematodes and Cestodes. Professor HENRY S. PRATT.

The American Toad (Bufo lentiginosus americanus, LeConte). NEWTON MILLER.

Observations on Copulation among Crawfishes with Special Reference to Sex Recognition. Dr. A. S. PEARSE.

Shorter Articles and Correspondence: Degeneration accompanying Inbreeding. Professor C. B. DAVENPORT. A Note of the Prairie-dog Owl which Resembles the Rattlesnake's Rattle: Dr. J. ARTHUR HARRIS.

Notes and Literature: The Causation of Sex, Professor H. E. JORDAN.

Index to Volume XLIII.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

Methods in Plant Histology

By CHARLES J. CHAMBERLAIN,

Second edition, revised and much enlarged ; 272 pages, with 88 illustrations, 8vo, cloth ; net $2.25, postpaid $2.39

THE first complete manual to be published on the subject of botanical microtechnique. It contains detailed directions for collecting and preparing plant material for microscopic investigation, setting forth the advantages and disadvantages of the different methods.

Will no doubt find a place in every well-regulated library, and will be found very useful by private students.—*Plant World.*

It is an excellent book for the individual worker and for classes in colleges.—*Education.*

A Laboratory Guide in Bacteriology

By PAUL G. HEINEMANN,

158 pages, interleaved, with 37 illustrations, 12mo, cloth ; net $1.50, postpaid $1.61

A CLEAR and concise presentation of bacteriological technique, designed principally as a manual for the medical student, but highly useful also as a reference book for the biological teacher and investigator, as well as for practical workers in the fields of medicine and hygiene.

The instruction given is clear and accurate, and the practical exercises are well selected.—*The Lancet* (London).

A book such as this must facilitate very greatly the practical class work, for which it is most excellently adapted. — *American Journal of Medical Sciences.*

The directions are clear and concise, and every stage is described so carefully that it is hard to see how the student can go astray. Physicians who are rusty in bacteriology cannot do better than buy this little book. The book is beautifully printed and bound.—*American Journal of Clinical Medicine.*

Animal Micrology:

Practical Exercises in Microscopical Methods

By MICHAEL F. GUYER,

250 pages, 8vo, cloth ; net $1.75, postpaid $1.88

THE title of this book will explain its scope. It is intended as a laboratory manual for textbook use. Its aim is to introduce the student to the technique of microscopic anatomy and embryology, emphasizing details of procedure rather than descriptions of reagents or apparatus. Sufficient account of the theoretical side of microscopy is given to enable the student to get satisfactory results from his microscope.

The directions are simple, explicit, and complete.—*American Journal of Clinical Medicine.*

The medical student will find it very useful as a guide to microscopic work.—*Journal of the American Medical Association.*

This is one of the cleanest works on microscopical technique we have ever seen, and is especially suitable for the beginner. It is full of points, tricks of technique not mentioned in other works, and is one that every student and physician should have.—*Medical Century.*

This valuable book is strong through its rigid exclusion of the trite and the conflicting. It is lucid and helpful, because a man long practiced in practical work has given what he believes the most expeditious and reliable method of obtaining a definite and comprehensive result. — *Medical Notes and Queries.*

A concise, eminently practical, and well-classified treatment.—*Science.*

The expositions of the methods recommended are admirably clear.—*Nature.*

One of the best and most practical works upon microscopic technique with which we are acquainted.—*American Naturalist.*

As a textbook it can hardly be improved. The research worker will find in this book just the information he frequently needs in preparing material with which he is not familiar.—*School Review.*

It does present in very clear form a judicious selection of methods, including an excellent untechnical account of the microscope and its optical principles, adequate for the undergraduate course in histology.— *Journal of Comparative Neurology and Psychology.*

ADDRESS DEPT. 64

Chicago THE UNIVERSITY OF CHICAGO PRESS New York

VOL. XLIV, NO. 518 FEBRUARY, 1910

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with
Special Reference to the Factors of Evolution

CONTENTS

Page

I. A Mendelian Interpretation of Variation that is Apparently Continuous. Professor EDWARD M. EAST 65

II. Color Inheritance in Lychnis dioica L. Dr. GEORGE HARRISON SHULL . 83

III. Is Regeneration a Repetition of the Ontogenetic and Phylogenetic Processes? SERGIUS MORGULIS 92

IV. Genetical Studies on Œnothera. BRADLEY MOORE DAVIS 108

V. Shorter Articles and Discussion:
The Mendelian View of Melanin Formation: DR. W. J. SPILLMAN . . 116

VI. Notes and Literature: Seton's Life History of Northern Animals, DR. J. A. ALLEN. Do Parthenogenetic Eggs of Hymenoptera produce only Males. A. FRANKLIN SHULL 124

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

TO ORNITHOLOGISTS AND MUSEUMS

W. F. H. ROSENBERG

Importer of Exotic Zoological Specimens

57 Haverstock Hill, N.W., England

Begs to announce the publication of a new Price List (No. 11) of **Bird Skins**. This catalogue contains over 5,000 species, and is the largest and most complete price list of birds ever published. It is arranged in systematic order, based on the classification of the British Museum "Catalogue of Birds," with authors' names, indications of localities, and an index to families. It will be sent gratis and post free on application, as will the following lists:

No. 7, Mammals; No. 8, Birds' Eggs;
No. 9, Reptiles, Amphibia, and Fishes.

Largest stock in the world of specimens in all branches of Zoology.

Specimens sent on approval.

Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

CONTENTS: Introduction, T. C. Chamberlin, Walker Museum; Fifty Years of Darwinism, Edward B. Poulton, Oxford University; The Theory of Natural Selection from the Standpoint of Botany, John M. Coulter, University of Chicago; Isolation as a Factor in Organic Evolution, David Starr Jordan, Stanford University; The Cell in Relation to Heredity and Evolution, Edmund B. Wilson, Columbia University; The Direct Influence of Environment, Dr. D. T. MacDougal, Carnegie Institution of Washington; The Behavior of Unit-Characters in Heredity, W. E. Castle, Harvard University; Mutation, Chas. B. Davenport, Station for Experimental Evolution, Cold Spring Harbor; Adaptation, Carl H. Eigenmann, Indiana University; Darwin and Paleontology, Henry Fairfield Osborn, Columbia University; Evolution and Psychology, G. Stanley Hall, Clark University.

Henry Holt & Company

34 West 33d St., New York
378 Wabash Ave., Chicago

THE
AMERICAN NATURALIST

Vol. XLIV *February, 1910* No. 518

A MENDELIAN INTERPRETATION OF VARIATION THAT IS APPARENTLY CONTINUOUS[1]

PROFESSOR EDWARD M. EAST

Harvard University

There are two objects in writing this paper. One is to present some new facts of inheritance obtained from pedigree cultures of maize; the other is to discuss the hypotheses to which an extension of this class of facts naturally leads. This discussion is to be regarded simply as a suggestion toward a working hypothesis, for the facts are not sufficient to support a theory. They do, however, impose certain limitations upon speculation which should receive careful consideration.

The facts which are submitted have to do with independent allelomorphic pairs which cause the formation of like or similar characters in the zygote. Nilsson-Ehle[2] has just published facts of the same character obtained from cultures of oats and of wheat. My own work is largely supplementary to his, but it had been given these interpretations previous to the publication of his paper.

In brief, Nilsson-Ehle's results are as follows: He found that while in most varieties of oats with black glumes blackness behaved as a simple Mendelian monohybrid, yet in one case there were two definite independent Mendelian unit characters, each of which was allelomorphic to its absence. Furthermore, in most varieties of oats having a ligule, the character behaved as a mono-hybrid dominant to absence of ligule, but in one case no less than four independent characters for presence of ligule, each being dominant to its absence, were found. In wheat a similar phenomenon occurred. Many crosses were made between varieties having red seeds and those having white seeds. In every case but one the F_2 generation gave the ordinary ratio of three red to one white. In the one exception—a very old red variety from the north of Sweden—the ratio in the F_2 generation was 63 red to 1 white. The reds of the F_2 generation gave in the F_3 generation a very close approximation to the theoretical expectation, which is 37 constant red, 8 red and white separating in the ratio of 63:1, 12 red and white separating in the ratio of 15:1, 6 red and white separating in the ratio of 3:1, and one constant white. He did not happen to obtain the expected constant white, but in the total progeny of 78 F_2 plants his other results are so close to the theoretical calculation that they quite convince one that he was really dealing with three indistinguishable but independent red characters, each allelomorphic to its absence. Nor can the experimental proof of the two colors of the oat glumes be doubted. The evidence of four characters for presence of ligule in the oat is not so conclusive.

---

[1] Contributions from the Laboratory of Genetics, Bussey Institution, Harvard University, No. 4. Read before the annual meeting of the American Society of Naturalists, Boston, December 29, 1909.

[2] Nilsson-Ehle, H. Kreuzungsuntersuchungen an Hafer und Weizen. Lunds Universitets Årsskrift, N. F. Afd. 2., Bd. 5, No. 2, 1909.

In my own work there is sufficient proof to show that in certain cases the endosperm of maize contains two indistinguishable, independent yellow colors, although in most yellow races only one color is present. There is also some evidence that there are three and possibly four independent red colors in the pericarp, and two colors in the aleurone cells. The colors in the aleurone cells when pure are easily distinguished, but when they are together they grade into each other very gradually.

Fully fifteen different yellow varieties of maize have been crossed with various white varieties, in which the crosses have all given a simple mono-hybrid ratio. In the other cases that follow it is seen that there is a di-hybrid ratio.

No. 5–20, a pure white eight-rowed flint, was pollinated by No. 6, a dent pure for yellow endosperm. An eight-rowed ear was obtained containing 159 medium yellow kernels and 145 light yellow kernels. The pollen parent was evidently a hybrid homozygous for one yellow which we will call Y_1 and heterozygous for another yellow Y_2. The gametes Y_1Y_2 and Y_1 fertilized the white in equal quantities, giving a ratio of approximately one medium yellow to one light yellow. The F_2 kernels from the dark yellow were as follows:

Table I.[3]

F_2 Seeds from Cross of No. 5–20, White Flint × No. 6 Yellow Dent. Homozygous for Y_1 and Heterozygous for Y_2

Dark Seeds Heterozygous for Both Yellows Planted

Ear No.	Dark Y.	Light Y.	Total Y.	No Y.
1	270	56	326	29
2	101	215	316	27
3	261	52	313	28
5	273	284	557	35
10	358	117	475	25
12	296	72	368	19
13	207	156	363	35
14	387	102	489	29
Total	2153	1054	3207	227
Ratio			14.1	1

The ratios of light yellows to dark yellows is very arbitrary, for there was a fine gradation of shades. The ratio of total yellows to white, however, is unmistakably 15 : 1.

In the next table (Table II) are given the results of F_2 kernels from the light yellows of F_1. Only ear No. 8, which was really planted with the dark yellows, showed yellows dark enough to be mistaken for kernels containing both Y_1 and Y_2. The remaining ears are clearly mono-hybrids with reference to yellow endosperm.

---

[3] In these tables only hand pollinated ears are given.

Table II.

F_2 Seeds from Same Cross as Shown in Table I

Light Yellow Seeds Heterozygous for Y_1 Planted

Ear No.	Dark Y.	Light Y.	No Y.
1		359	117
2		144	54
3		173	63
4		433	136
6		316	120
8	331		109
8a		229	86
9		325	115
10		227	87
11[4]		4	434
12		318	118
13		256	93
Total		3111	1098
Ratio		2.8	1

In a second case the female parent possessed the yellow endosperm. No. 11, a twelve-rowed yellow flint, was crossed with No. 8, a white dent. The F_2 kernels in part showed clearly a mono-hybrid ratio, and in part blended gradually into white. Two of these indefinite ears proved in the F_3 generation to have had the 15:1 ratio in the F_2 generation. Ear 7 of the F_2 generation calculated from the results of the entire F_3 crop must have had about 547 yellow to 52 white kernels, the theoretical number being 561 to 31. The hand-pollinated ears of the F_3 generation (yellow seeds) gave the results shown in Table III.

The F_3 generation grown from the other ear, Ear No. 8, showed that the ratio of yellows to whites in the F_2 generation was about 227 to 47. As the theoretical ratio is 257 to 17, the ratio obtained is somewhat inconclusive. A classification of the open field crop could not be made accurately on account of the light color of the yellows and

---

[4] Discarded from average. This ear evidently grew from one kernel of the original white mother that was accidentally self-pollinated. The four yellow kernels all show zenia from accidental pollination in the next generation.

TABLE III.

No. 11 YELLOW × No. 8 WHITE

F_3 Generation from Yellow Seeds of F_2 Generation

Ear No.	Dark Y.	Light Y.	Total Y.	No Y.	Ratio They Approximate.
1	116	95	211	19	15Y : 1 no Y
14			88	5	15Y : 1 no Y
5	181	122			$3Y_1Y_2 : 1\ Y_{1 \text{ or } 2}$
4		253		68	3Y : 1 no Y
6		193		73	"
8		163		79	"
11		108		35	"
9		456			Constant $Y_{1 \text{ or } 2}$

the presence of many kernels showing zenia. Table IV, however, showing the hand-pollinated kernels of the interbred yellows of the F_2 generation, settles beyond a doubt the fact that the two yellows were present.

TABLE IV.

PROGENY OF EAR NO. 8 OF THE SAME CROSS AS SHOWN IN TABLE III

F_3 Generation from Yellow Seeds of F_2 Generation

Ear No.	Dark Y.	Light Y.	Total Y.	No Y.	Ratio They Approximate.
10	101	188	289	25	15Y : 1 no Y
11	89	219	308	23	15Y : 1 no Y
3		233			constant light Y
9	dark and light		331		3 dark : 1 light Y
13	dark and light		350		3 dark : 1 light Y
8		294		108	3 light : 1 no Y
15		221		87	3 light : 1 no Y
1[5]		197		203	

In a third case an eight-rowed yellow flint, No. 22, was crossed with a white dent, No. 8. Only four selfed ears were obtained in the F_2 generation. Ear 1 had 72 yellow to 37 white kernels. This ear was poorly developed and undoubtedly had some yellow kernels which were classed as whites. Ear 4 had 158 yellow and 42 white kernels. It is very likely that both of these ears were mono-hybrids, but the F_3 generation was not grown. Ear 5 had 148 yellow and 15 white kernels. Ear 7 had 78 yellow and 5 white kernels. It seems probable that both of these ears were di-hybrids, but only Ear 5 was grown another generation. The kernels classed as white proved to be pure; the open field crop from the yellow kernels gave 14 pure yellow ears and 14 hybrid yellow. Theoretically the ratio should be 7 pure yellows (that is, pure for either one or both yellows) and 8 hybrid yellows (4 giving 15 yellows to 1 white and 4 giving 3 yellows to 1 white). Five hand-pollinated selfed ears were obtained. Three of these gave mono-hybrid ratios, with a total of 607 yellows to 185 white kernels. One ear was a pure dark yellow (probably $Y_1Y_1Y_2Y_2$). The other ear was poorly filled, but had 27 dark yellows (probably Y_1Y_2) and 7 light yellow kernels (Y_1 or Y_2). Unfortunately no 15:1 ratio was obtained in this generation, but this is quite likely to happen when only five selfed ears are counted. The gradation of colors and the general appearance of the open field crop, however, lead me to believe that we were again dealing with a di-hybrid.

---

[5] Kernel from which this ear grew was evidently pollinated by no Y.

Two yellows appeared in still another case, that of white sweet No. 40♀ × yellow dent No. 3♂. Only one selfed ear was obtained in the F_2 generation giving 599 yellow to 43 white kernels. Of these kernels 486 were starchy and 156 sweet, which complicated matters in the F_3 generation because it was very difficult to separate the light yellow sweet from the white sweet kernels. Among the selfed ears were three pure to the starchy character, and in these ears the dark yellows, the light yellows and whites stood out very distinctly. Ear 12 had 156 dark yellow; 47 light yellow; 14 white kernels. Ear 13 had 347 dark yellow; 93 light yellow; 25 white kernels. The third starchy ear, No. 6, had 320 light yellow; 97 white kernels. Two ears, therefore, were di-hybrids, and one ear a mono-hybrid.

The ears which were heterozygous for starch and no starch and those homozygous for no starch, could not all be classified accurately, but it is certain that some pure dark yellows, some pure light yellows, some showing segregation of yellows and whites at the ratio 15:1, and some showing segregation of yellows and whites at the ratio of 3:1, were obtained,

One other case should be mentioned. One ear of a dent variety of unknown parentage obtained for another purpose was found to have some apparently heterozygous yellow kernels. Seven selfed ears were obtained from them, of which two were pure yellow. The other five ears each gave the di-hybrid ratio. There was a total of 1906 yellow seeds to 181 white seeds, which is reasonably close to the expected ratio, 1956 yellow to 131 white.

It is to be regretted that I can present no other case of this class that has been fully worked out, although several other characters which I have under observation in both maize and tobacco seem likely to be included ultimately. Nevertheless, the fact that we have to deal with conditions of this kind in studying inheritance is established; granting only that they will be somewhat numerous, it opens up an entirely new outlook in the field of genetics.

In certain cases it would appear that we may have several allelomorphic pairs each of which is inherited independently of the others, and each of which is separately capable of forming the same character. When present in different numbers in different individuals, these units simply form quantitative differences. It may be objected that we do not know that two colors that appear the same physically are exactly the same chemically. That is true; but Nilsson-Ehle's case of several unit characters for presence of ligule in oats is certainly one where each of several Mendelian units forms exactly the same character. It may be that there is a kind of biological isomerism, in which, instead of molecules of the same formula having different physical properties, there are isomers capable of forming the same character, although, through difference in construction, they are not allelomorphic to each other. At least it is quite a probable supposition that through imperfections in the mechanism of heredity an individual possessing a certain character should give rise to different lines of descent so that in the F_n generation when individuals of these different lines are crossed, the character behaves as a di-hybrid instead of as a mono-hybrid. In other words, it is more probable that these units arise through variation in different individuals and are combined by hybridization, than that actually different structures for forming the same character arise in the same individual.

On the other hand, there is a possibility of an action just the opposite of this. Several of these quantitative units which produce the same character may become attached like a chemical radical and again behave as a single pair. Nilsson-Ehle gives one case which he does not attempt to explain, where the same cross gave a 4:1 ratio in one instance and 8.4:1 ratio in another instance. In his other work characters always behaved the same way; that is, either as one pair, two pairs, three pairs, etc. In my work, the yellow endosperm of maize has behaved differently in the same strain, but it is probably because the yellow parent is homozygous for one yellow and heterozygous for the other. They were known to be pure for one yellow, but it would take a long series of crosses to prove purity in two yellows.

Let us now consider what is the concrete result of the inter-action of several cumulative units affecting the same character. Where there is simple presence dominant to absence of a number n of such factors, in a cross where all are present in one parent and all absent in the other parent, there must be 4^n individuals to run an even chance of obtaining a single F_2 individual in which the character is absent. When four such units, $A_1A_2A_3A_4$ are crossed with $a_1a_2a_3a_4$, their absence, only one pure recessive is expected in 256 individuals. And 256 individuals is a larger number than is usually reported in genetic publications. When a smaller population is considered, it will appear to be a blend of the two parents with a fluctuating variability on each side of its mode. Of course if there is absolute dominance and each unit appears to affect the zygote in the same manner that they do when combined, the F_2 generation will appear like the dominant parent unless a very large number of progeny are under observation and pure recessives are obtained. This may be an explanation of the results obtained by Millardet; it is certainly as probable as the hypothesis of the non-formation of homozygotes. Ordinarily, however, there is not perfect dominance, and variation due to heterozygosis combined with fluctuating variation makes it almost impossible to classify the individuals except by breeding. The two yellows in the endosperm of maize is an example of how few characters are necessary to make classification difficult. First, there is a small amount of fluctuation in different ears due to varying light conditions owing to differences in thickness of the husk; second, all the classes having different gametic formulæ differ in the intensity of their yellow in the following order, $Y_1Y_1Y_2Y_2$, $Y_1y_1Y_2Y_2$ or $Y_1Y_1Y_2y_2$, Y_1Y_1, Y_2Y_2, Y_1y_1, Y_2y_2, y_1y_2. As dominance becomes less and less evident, the Mendelian classes vary more and more from the formula $(3+1)^n$, and approach the normal curve, with a regular gradation of individuals on each side of the mode. When there is no dominance and open fertilization, a state is reached in which the curve of variation simulates the fluctuation curve, with the difference that the gradations are heritable.

One other important feature of this class of genetic facts must be considered. If units $A_1A_2A_3a_4$ meet units $a_1a_2a_3A_4$, in the F_2 generation there will be one pure recessive, $a_1a_2a_3a_4$, in every 256 individuals. This explains an apparent paradox. Two individuals are crossed, both seemingly pure for presence of the same character, yet one individual out of 256 is a pure recessive. When we consider the rarity with which pure dominants or pure recessives (for all characters) are obtained when there are more than three factors, we can hardly avoid the suspicion that here is a perfectly logical way of accounting for many cases of so-called atavism. Furthermore, many apparently new characters may be formed by the gradual dropping of these cumulative factors without any additional hypothesis. For example, in *Nicotiana tabacum* varieties there is every gradation[6] of loss of leaf surface near the base of the sessile leaf, until in *N. tabacum fruticosa* the leaf is only one step removed from a petioled condition. If this step should occur the new plant would almost certainly be called a new species; yet it is only one degree further in a definite series of loss gradations that have already taken place. If it should be assumed that in other instances slight qualitative as well as quantitative changes take place as units are added, then it becomes very easy, theoretically, to account for quite different characters in the individual homozygous for presence of all dominant units, and in the individual in which they are all absent.

Unfortunately for these conceptions, although I feel it extremely probable that variations in *some* characters that seem to be continuous will prove to be combinations of segregating characters, it is exceedingly difficult to demonstrate the matter beyond a reasonable doubt. As an illustration of the difficulties involved in the analysis of pedigree cultures embracing such characters, I wish to discuss some data regarding the inheritance of the number of rows of kernels on the maize cob.

The maize ear may be regarded as a fusion of four or more spikes, each joint of the rachis bearing two spikelets. The rows are, therefore, distinctly paired, and no case is known where one of the pair has been aborted. This is a peculiar fact when we consider the great number of odd kinds of variations that occur in nature. The number of rows per cob has been considered to belong to continuous variations by DeVries, and a glance at the progeny from the seeds of a single selfed ear as shown in Table V seems to confirm this view.

There is considerable evidence, however, that this character is made up of a series of cumulative units, inde-

---

[6] It is not known at present how this character behaves in inheritance.

TABLE V.

PROGENY OF A SELFED EAR OF LEAMING MAIZE HAVING 20 ROWS

Classes of rows	12	14	16	18	20	22	24	26	28	30
No. of ears	1	0	5	4	53	35	19	5	2	1

pendent in their inheritance. There is no reason why it should not be considered to be of the same nature as various other size characters in which variation seems to be continuous, but in which relatively constant gradations may be isolated, each fluctuating around a particular mode. But this particular case possesses an advantage not held by most phenomena of its class, in that there is a definite discontinuous series of numbers by which each individual may be classified.

Previous to analyzing the data from pedigree cultures, however, it is necessary to take into consideration several facts. In the first place, what limits are to be placed on fluctuations?[7] From the variability of the progeny of single ears of dent varieties that have been inbred for several generations, it might be concluded that the deviations are very large. But this is not necessarily the case; these deviations may be due largely to gametic structure in spite of the inbreeding, since no conscious selection of homozygotes has been made. There is no such variation in eight-rowed varieties, which may be considered as the last subtraction form in which maize appears and therefore an extreme homozygous recessive. In a count of the population of an isolated maize field where Longfellow, an eight-rowed flint, had been grown for many years, 4 four-rowed, 993 eight-rowed, 2 ten-rowed and 1 twelve-rowed ears were found. Only seven aberrant ears out of a thousand had been produced, and some of these may have been due to vicinism.

On the other hand a large number of counts of the number of rows of both ears on stalks that bore two ears has shown that it is very rare that there is a change greater than ± 2 rows. If conditions are more favorable at the time when the upper ear is laid down it will have two more rows than the second ear; if conditions are favorable all through the season, the ears generally have the same number of rows; while if conditions are unfavorable when the upper ear is laid down, the lower ear may have two more rows than the upper ear. Furthermore, seeds from the same ear have several times been grown on different soils and in different seasons, and in each case the frequency distribution has been the same. Hence it may be concluded that in the great majority of cases fluctuation is not greater than in ± 2 rows, although fluctuations of ± 4 rows have been found.

---

[7] The word fluctuation is used to designate the somatic changes due to immediate environment, and which *are not inherited.*

A second question worthy of consideration is: Do somatic variations due to varying conditions during development take place with equal frequency in individuals with a large number of rows and in individuals with a small number of rows? From the fact that several of my inbred strains that have been selected for three generations for a constant number of rows, increase directly in variability as the number of rows increases, the question should probably be answered in the negative. This answer is reasonable upon other grounds. The eight-rowed ear may vary in any one of four spikes, the sixteen-rowed ear may vary in any one of eight spikes; therefore the sixteen-rowed ear may vary twice as often as the eight-rowed ear. By the same reasoning, the sixteen-rowed ear may sometimes throw fluctuations twice as wide as the eight-rowed ear.

A third consideration is the possibility of increased fluctuation due to hybridization. Shull[8] and East[9] have shown that there is an increased stimulus to cell division when maize biotypes are crossed—a phenomenon apart from inheritance. There is no evidence, however, that increased gametic variability results. Johannsen[10] has shown that there is no such increase in fluctuation when close-pollinated plants are crossed. I have crossed several distinct varieties of maize where the modal number of rows of each parent was twelve, and in every instance the F_1 progeny had the same mode and about the same variability.

---

[8] Shull, G. H., "A Pure-line Method in Corn Breeding," *Rept. Amer. Breeders' Assn.*, 5, 51–59, 1909.

[9] East, E. M., "The Distinction between Development and Heredity in Inbreeding," AMER. NAT., 43, 173–181, 1909.

Finally, a possibility of gametic coupling should be considered. Our common races of flint maize all have a low number of rows, usually eight but sometimes twelve; dent races have various modes running from twelve to twenty-four rows. When crosses between the two subspecies are made, the tendency is to separate in the same manner.

Attention is not called to these obscuring factors with the idea that they are universally applicable in the study of supposed continuous variation. But there are similar conditions always present that make analysis of these variations difficult, and the facts given here should serve to prevent premature decision that they do not show segregation in their inheritance.

Table VI shows the results from several crosses between maize races with different modal values for number of rows. Several interesting points are noticeable. The modal number is always divisible by four. This is also the case with some twenty-five other races that I have examined but which are not shown in the table. I suspect that through the presence of pure units zygotes having a multiple of four rows are formed, while heterozygous units cause the dropping of two rows. The eight-rowed races are pure for that character, the twelve-rowed races vary but little, but the races having a higher number of rows are exceedingly variable.

When twelve-rowed races are crossed with those having eight rows, the resulting F_1 generation always—or nearly

---

[10] Johannsen, W., "Does Hybridization Increase Fluctuating Variability?" *Rept. Third Inter. Con. on Genetics*, 98–113, London, Spottiswoode, 1907.

Table VI.

Crosses between Maize Strains with Different Numbers of Rows

Parents. (Female Given First.)	Gen.	Row Classes.						
		8	10	12	14	16	18	20
Flint No. 5		100						
Flint No. 11		1	4	387	7	1		
Flint No. 24		100						
Flint No. 15		100						
Dent No. 6				6	31	51	18	4
Dent No. 8			3	54	36	12	2	
Sweet No. 53[11]		1	5	25	4			
Sweet No. 54[11]		25	2	1				
No. 5 × No. 53	F_1	1	7	13				
No. 5 × No. 6	F_1	11	18	27	3			
No. 11 × No. 5	F_1	2	4	18				
No. 11 × No. 53	F_1	2	5	17				
No. 24 × No. 53	F_1	57	8	3				
No. 15 × No. 8	F_1	1	14	26	3	1		
No. 15 × No. 8 (from 10-row ear)	F_2	14	15	28	9	1		
No. 15 × No. 8 (from 12-row ear)	F_2	4	13	25	6	3		
No. 8 × No. 54	F_1	1	6	14				
No. 8 × No. 54 (from 12-row ear)	F_2	11	25	38	2	1		

always—has the mode at twelve rows. In one case cited in Table VI, No. 24 × No. 53, nearly all the F_1 progeny were eight-rowed. It might appear from this, either that the low number of rows was in this case dominant, or that the female parent has more influence on the resulting progeny than the male parent. I prefer to believe, however, that the individual of No. 53 which furnished the pollen was due to produce eight-rowed progeny. Unfortunately no record was kept of the ear borne by this plant, but No. 53 sometimes does produce eight-rowed ears.

When a race with a mode higher than twelve is crossed with an eight-rowed race, the F_1 generation is always intermediate, although it tends to be nearer the high-rowed parent. Only one example is given in the table, but it is indicative of the class. These results are rather confusing, for there seems to be a tendency to dominance in the twelve-rowed form that is not found in the forms with a higher number of rows. I have seen cultures of other investigators where 12-row × 8-row resulted in a ten-rowed F_1 generation, so the complication need not worry us at present.

---

[11] Approximately.

The results of the F_2 generation show a definite tendency toward segregation and reproduction of the parent types. I might add that in at least two cases I have planted extracted eight-rowed ears and have immediately obtained an eight-rowed race which showed only slight departures from the type. Selection from those ears having a high number of rows has also given races like the high-rowed parent without recrossing with it. It is regretted that commercial problems were on hand at the time and no exact data were recorded. It can be stated with confidence, however, that ears like each parent are obtained in the F_2 generation, from which with care *races* like each parent may be produced. *Segregation seems to be the best interpretation of the matter.*

These various items may seem disconnected and uninteresting, but they have been given to show the tangible basis for the following theoretical interpretation. No hard and fast conclusion is attempted, but I feel that this interpretation with possibly slight modifications will be found to aid the explanation of many cases where variation is apparently continuous.

Suppose a basal unit to be present in the gametes of all maize races, this unit to account for the production of eight rows. Let additional independent interchangeable units, each allelomorphic to its own absence, account for each additional four rows; and let the heterozygous condition of any unit represent only half of the homozygous condition, or two rows. Then the gametic condition of a homozygous twenty-rowed race would be $8 + AABBCC$, each letter actually representing two rows. When crossed with an eight-rowed race, the F_2 generation will show ears of from eight to twenty rows, each class being represented by the number of units in the coefficients in the binomial expansion where the exponent is twice the number of characters, or in this case $(a + b)^6$.

The result appears to be a blend between the characters of the two parents with a normal frequency distribution of the deviants. Only one twenty-rowed individual occurs in 64 instead of the 27 expected by the interaction of three dominant factors in the usual Mendelian ratios. The remainder of the 27 will have different numbers of rows, and, by their gametic formulæ, different expectations in future breeding as follows:

1 $AABBCC = 20$ rows.
2 $AaBBCC = 18$ rows.
2 $AABbCC = 18$ rows.
2 $AABBCc = 18$ rows.
4 $AaBbCC = 16$ rows.
4 $AaBBCc = 16$ rows.
4 $AABbCc = 16$ rows.
8 $AaBbCc = 14$ rows.

There are four visibly different classes and eight gametically different classes. It must also be remembered that the probability that the original twenty-rowed ear in actual practise may have had more than three units in its gametes has not been considered. This point is illustrated clearly if we work out the complete ratio for the three characters, and note the number of gametically different classes which compose the modal class of fourteen rows in Table VII. It actually contains seven gametically different classes and not a single homozygote. If this conception of independent allelomorphic pairs affecting the same character proves true, it will sadly upset the biometric belief that the modal class is *the type* around which the variants converge, for there is actually less chance of these individuals breeding true than those from *any other* class.

TABLE VII

THEORETICAL EXPECTATION IN F_2 WHEN A HOMOZYGOUS TWENTY-ROWED MAIZE EAR IS CROSSED WITH AN EIGHT-ROWED EAR

Classes	8	10	12	14	16	18	20
No. ears	1	6	15	20	15	6	1

The conception is simple and is capable theoretically of bringing in order many complicated facts, although the presence of fluctuating variation will be a great factor in preventing analysis of data. I have thought of only one fact that is difficult to bring into line. If $8AA$, $8BB$ and $8CC$ all represent homozygous twelve-rowed ears—to continue the maize illustration—and none of these factors are allelomorphic to each other, sixteen-rowed ears should sometimes be obtained when crossing two twelve-rowed ears. I am not sure but that this would happen if we were to extract all the homozygous twelve-rowed strains after a cross between sixteen-row and eight-row, and after proving their purity cross them. In some cases the additional four-row units would probably be allelomorphic to each other and in other cases independent of each other. On the other hand, this is only an hypothesis, and while I have faith in its foundation facts, the details may need change.

Castle has raised the point that greater variation should be expected in the F_1 generation than in the P_1 generations when crossing widely deviating individuals showing variation apparently continuous. If the parents are strictly pure for a definite number of units, say for size, a greater variation should certainly be expected in the F_1 generation after crossing. But considering the difficulties that arise when even five independent units are considered, can it be said that anything has heretofore been known concerning the actual gametic status of parents which it is known do vary in the character in question and in which the variations are inherited, for the race can be changed by selection within it. It may be, too, that the correct criterion has not been used in size measurements, for, as others have suggested, solids vary as the cube root of their mass, whereas the sum of the weights of the body cells has usually been measured and compared directly with similar sums.

Attention should be called to one further point. Many characters in all probability are truly blending in their inheritance, but there is another interpretation which may apply in certain cases. I have repeatedly tried to cross Giant Missouri Cob Pipe maize (14 feet high) and Tom Thumb pop maize (2 feet high), but have always failed. They both cross readily with varieties intermediate in size, but are sterile between themselves. We may imagine that the gametes of each race, though varying in structure, are all so dissimilar that none of them can unite to form zygotes. Other races may be found where only part of the gametes of varying structure are so unlike that they will not develop after fusion. The zygotes that do develop will be from those more alike in construction. An apparent blend results, and although segregation may take place, no progeny as extreme as either of the parents will ever occur.

I may say in conclusion that the effect of the truth of this hypothesis would be to add another link to the increasing chain of evidence that the word mutation may properly be applied to any inherited variation, however small; and the word fluctuation should be restricted to those variations due to immediate environment which do not affect the germ cells, and which—it has been shown—are not inherited. In addition it gives a rational basis for the origin of *new* characters, which has hitherto been somewhat of a Mendelian stumbling-block; and also gives the term unit-character less of an irrevocably-fixed-entity conception, which is more in accord with other biological beliefs.

COLOR INHERITANCE IN LYCHNIS DIOICA L.[1]

DR. GEORGE HARRISON SHULL

Two years ago I showed that in *Lychnis dioica* L. the purple-flowered form behaves in normal Mendelian manner when crossed with the same type or with the typically white-flowered form of the same species (Shull, 1908). In subsequent work it has been discovered that the purple-flowered plants do not form a single unit-group, but that there are at least two distinct types, one of which has more bluish-purple flowers, the other more reddish-purple. No notice had been taken of such variation in the color characters until last year, although it had been observed that there was some variation in the intensity of color in different plants, and these had been, to a slight extent, recorded in terms of intensity, *e. g.*, as "light," "medium" and "dark." Last year several individuals were observed so noticeably distinct because of the bluish character of their flowers, that an effort was made to determine the relationship of this light bluish-purple color to the more common reddish-purple, and several crosses were made representing the combination of "blue" and "red," using a single red-flowered indi-

TABLE I

Ped. No.	Cross.	Red.	Blue.	White.	Theoretical Result.	Ratio Involved.
0845	Blue × Blue	1	83	0	0 : 84 : 0	0 : 1 : 0
0846	Blue × Red	47	49	0	48 : 48 : 0	1 : 1 : 0
0844	Blue × White	52	0	46	49 : 0 : 49	1 : 0 : 1
0849	Red × Red	68	22	1	68 : 23 : 0	3 : 1 : 0
0848	Red × Blue	27	32	27	32 : 32 : 22	3 : 3 : 2
0847	Red × White	53	0	46	50 : 0 : 49	1 : 0 : 1
0875	White × Blue	34	24	41	25 : 25 : 49	1 : 1 : 2
0876	White × Red	31	20	0	38 : 13 : 0	3 : 1 : 0
	Total	313	230	161	310 : 225 : 169	

---

[1] Read before the Botanical Society of America at Boston, December, 1909.

vidual as the mother in one series of crosses, and a single blue-flowered individual as the mother in another series. The same blue-flowered and red-flowered plants were also crossed at the same time with white-flowered plants. The actual and theoretical results of these eight crosses are given in Table I.

In addition to these families which were bred in such a way as to allow the definite working out of the gametic formulæ of the parents and the theoretical results, bluish-flowered plants were also observed in a number of other pedigrees. In some of these families only a small proportion of the individuals had their tints recorded, as they were being especially studied with other objects in view. Such fragmentary records are of no special value in this connection, of course, and they will not be presented; but in Table II. are given all those pedigrees in which approximately all the purple-flowered offspring were recorded either as "blue" or "red."

In this second table it is impossible to vouch for the correctness of the suggested theoretical results, as the gametic formulæ of the parents are in each case very imperfectly known. The column of theoretical results is constructed simply by using that one of the available theoretical ratios which fits most accurately the observed facts. When numbers are so small, mere inspection can not determine with certainty which is the correct theoretical ratio. Thus in No. 08168 the empirical ratio, 19:11:31, is almost equally well referred to either of the available ratios, 1:1:2 and 3:1:4, as it stands about midway between them. Notwithstanding the fact that ignorance of the gametic composition of the parents in this second table makes it impossible to decide in all cases what ratio should have been expected, the results harmonize well throughout with those which comprise Table I., where the theoretical "expectation" is definitely known.

All of the crosses recorded in these two tables seem to be typically Mendelian, with the bluish-purple color hypo-

TABLE II

Ped. No.	Cross.	Red.	Blue.	White.	Probable Theoretical Result.	Ratio Invoked.
0850	Red × Red	67	0	0	67 : 0 : 0	1 : 0 : 0
0851	Red × White	40	13	0	40 : 13 : 0	3 : 1 : 0
0852	White × Red	26	4	52	23 : 8 : 51	9 : 3 : 20
0853	Red × Red	82	0	19	76 : 0 : 25	3 : 0 : 1
0855	Red × Red	105	0	0	105 : 0 : 0	1 : 0 : 0
0856	Red × White	39	18	39	36 : 12 : 48	3 : 1 : 4
0857	Red × Red	64	14	25	58 : 19 : 26	9 : 3 : 4
0858	Red × White	17	12	33	16 : 15 : 31	1 : 1 : 2
0859	Red × White	10	0	14	9 : 0 : 15	3 : 0 : 5
0860	Red × Red	77	0	21	74 : 0 : 24	3 : 0 : 1
0861	Red × White	38	0	0	38 : 0 : 0	1 : 0 : 0
0862	Red × Red	101	0	0	101 : 0 : 0	1 : 0 : 0
0863	Red × Red	30	0	6	27 : 0 : 9	3 : 0 : 1
0864	Red × White	3	0	13	4 : 0 : 12	1 : 0 : 3
0865	White × Red	18	0	6	18 : 0 : 6	3 : 0 : 1
0866	White × Red	37	0	29	33 : 0 : 33	1 : 0 : 1
0867	White × Red	25	0	16	20 : 0 : 21	1 : 0 : 1
0868	Red × Red	74	0	12	65 : 0 : 21	3 : 0 : 1
0869	Red × White	44	0	49	47 : 0 : 46	1 : 0 : 1
0871	White × Red	30	0	54	31 : 0 : 53	3 : 0 : 5
0882	White × Red	23	8	43	21 : 7 : 46	9 : 3 : 20
0884	White × Red	26	8	40	28 : 9 : 37	3 : 1 : 4
08100	White × Red	44	0	45	44 : 0 : 45	1 : 0 : 1
08105	White × Red	29	0	29	29 : 0 : 29	1 : 0 : 1
08150	Red × White	23	27	35	21 : 21 : 43	1 : 1 : 2
08155	Red × Red	25	0	0	25 : 0 : 0	1 : 0 : 0
08156	White × Red	29	16	34	30 : 10 : 39	3 : 1 : 4
08161	Red × Red	44	13	18	42 : 14 : 19	9 : 3 : 4
08162	Red × White	48	0	45	47 : 0 : 46	1 : 0 : 1
08168	White × Red	19	11	31	15 : 15 : 31	1 : 1 : 2
08175	Red × Red	70	0	29	74 : 0 : 25	3 : 0 : 1
08177	Red × Red	72	0	22	71 : 0 : 23	3 : 0 : 1
08178	Red × White	47	0	47	47 : 0 : 47	1 : 0 : 1
	Total	1,426	144	806	1,382 : 143 : 851	

static or "recessive" to the red. This is one of the first cases of this kind which has appeared, as heretofore the bluish colors have quite generally been found epistatic to the reds. The most important studies which have been made relating to the inheritance of the anthocyan colors are those of Bateson (1902, 1905, 1906, 1909) and his co-workers, on *Lathyrus* and *Matthiola*, Miss Wheldale (1907) and Baur (1908) on *Antirrhinum*, and Tschermak (1901, 1904) on *Pisum* and *Phaseolus*. In all of these genera as well as in *Clarkia* and *Salvia* (Bateson, etc., 1905), the more bluish anthocyan color is epistatic to the reddish anthocyan. Bateson (1909, p. 41) states in one place, that in *Primula Sinensis* "blue is hypostatic to all the red shades,'' although the magenta colors are shown to be epistatic to red. This isolated statement regarding the blue color in *Primula Sinensis* is not supported by any data, and I do not know the chemical relation between it and the magenta colors. Miss Wheldale (1909), who discusses at some length the color series in *Primula* material secured from Bateson and Gregory, makes no mention of the occurrence of blue, though she ascribes the production of magenta and crimson to the action of a ''bluing factor'' upon red anthocyan.

Upon comparison of my bluish-purple *Lychnis* with the colored plates of *Primula* given by Bateson (1909, p. 294) I think the *Lychnis* color should be classed as a light magenta rather than a blue, as there is a decided reddish element in this *Lychnis* color. If Bateson's isolated statement that ''blue is hypostatic to all the red shades'' in *Primula* is correct, then that color corresponds in its behavior with this light magenta color in *Lychnis*. I have not made a thorough investigation of the chemical relations of the two types of purple in *Lychnis*, but have demonstrated by a few preliminary tests that the reddish-purple color is converted to bluish when treated with alkalies, and that the light bluish-purple is made as bright red as the red-purple type on treating with weak acids, thus indicating a very simple relation between these two colors.

Although the relation between the two types of color in *Lychnis* is just the reverse of that exhibited by practically all other plants in which similar colors have been studied, I am led to essentially the same conclusions regarding the method of color determination, as those derived from the extensive studies which have been made on *Lathyrus*, *Matthiola*, etc. The production of the ''lowest stage'' of color, *i. e.*, the color which results from the combined action of the least number of genes, is due to the interaction of two independent factors or genes, either of which produces no color when not associated with the other. In order to produce a second stage of color it is necessary to assume the occurrence of a third gene which can make its characteristic color-reaction apparent only in the presence of the other two. Thus in *Lathyrus*, etc., it was assumed that two factors, *R* and *C*, are necessary to the production of a red anthocyan color, and that a third factor, *B*, modifies this color to bluish. This assumption requires that the presence of each of these three genes be dominant over its absence. An alternative assumption might have been made, viz., that the absence of the third factor is dominant over its presence. Then the lowest grade of color would be a *blue* color produced by the simultaneous presence of *B* and *C*, and the red color would appear only when *R* is present in the homozygous state.

Last year in my discussion of the presence and absence hypothesis (Shull, 1909) it was pointed out that it would be impossible in many cases to determine "whether red flowers are blue flowers with an added factor for acidity or whether blue flowers are red with an added factor for alkalinity," and also that "it is conceivable that both these situations may be presented in different species." The color characters in *Lychnis* give a very good illustration of these statements.

If we assume the dominance of presence over absence, the lowest grade of color—the bluish—is formed by the combined action of two genes, *B* and *C*, the one probably representing, according to the studies of Miss Wheldale (1909), the capacity to produce a chromogen of the flavone series, the other representing the production of an oxidase. The red color is in this case produced by an added factor, *R*, which modifies the bluish color produced by *B* and *C*. The *R* may be perhaps an acidifier, a reducing agent, or a partial inhibitor of the oxidizing action of *B*. This method of explaining color inheritance in *Lychnis* presents an interesting reversal of the places occupied by *R* and *B* when compared with the situation in other plants.

If, on the other hand, the assumption be made that, in *Lychnis,* absence of B is dominant over its presence, the relative positions of R and B may remain the same as in *Lathyrus, Matthiola,* etc. For in this case R and C will be the two factors necessary to the production of red anthocyan and B the "bluing factor" which is added to it to form bluish anthocyan, the difference between *Lychnis* and *Lathyrus* being simply that the B which may be looked upon perhaps as a factor for alkalinity or for an oxidizer, is too weak in its activity in *Lychnis* to produce its characteristic effect except when present in double quantity or strength, as it is when in the homozygous state.

The data now at hand do not make possible a decision as to whether presence, or absence of the color-modifier, is dominant in *Lychnis,* as each of these assumptions may be shown to fit all the facts involved in Table I. The gametic formulæ of the six plants involved in these eight crosses are presented in Table III., to enable a comparison of the two methods of explanation.

TABLE III

Ped. No.	Crosses.	$B + C$ Produces Blue. Presence of R Dominant.	$R + C$ Produces Red. Absence of B Dominant.	Resultant Ratio Red : Blue : White.
0845	Blue × Blue	$BCC \times BBC$	$BBRCC \times BBRRC$	0 : 1 : 0
0846	Blue × Red	$BCC \times RBBCC$	$BBRCC \times BRRCC$	1 : 1 : 0
0844	Blue × White	$BCC \times RR\ (CC?)$	$BBRCC \times CC$	1 : 0 : 1
0849	Red × Red	$RB(B?)C \times RBBCC$	$BRC \times BRRCC$	3 : 1 : 0
0848	Red × Blue	$RB(B?)C \times BBC$	$BRC \times BBRRC$	3 : 3 : 2
0847	Red × White	$RB(B?)C \times RR(CC$ if ♀ $= RBC)$	$BRC \times CC$	1 : 0 : 1
0875	White × Blue	$RB(B?) \times BBC$	$B \times BBRRC$	1 : 1 : 2
0876	White × Red	$RB(B?) \times RBBCC$	$B \times BRRCC$	3 : 1 : 0

The fact now demonstrated that the purple color in *Lychnis* is due to the presence of at least three distinct genes instead of only one, as originally assumed by me, has served to elucidate several difficulties which had been encountered. It may be recalled that a rather large range of supposedly fluctuating variability in the percentage of purple-flowered individuals in families resulting from crosses of purple with white was shown to form a normal probable error curve, thus conforming very well with the Mendelian hypothesis that gametes of different alternative composition unite according to the laws of chance. While this conclusion is not in any way opposed by my later studies, it is now known that a portion of that apparently fluctuating variation may have been due to the occurrence of a mixture of several different ratios. In accordance with the present demonstration that the purple color is due to three factors, the combined action of two of which are necessary to the production of any color and the addition of a third for the modification of this color, a cross between white and purple must give either all purple, or purple and white in any of the following ratios: 3:1, 1:1, 3:5, or 1:3, though the ratio 1:1 occurs much more frequently than any of the other possibilities. In other words, without any fluctuation at all, purple-flowered individuals, when mated entirely at random with white-flowered individuals, should produce progenies consisting of 25, 37.5, 50, 75 or 100 per cent. purple-flowered offspring, instead of only 50 or 100 per cent.

I have in several cases found purple-flowered individuals among the offspring of two white-flowered parents. Such occurrence was entirely incomprehensible to me except on the basis of an error in technique. It now becomes obvious that white crossed with white must occasionally give various proportions of purple-flowered offspring. Some such crosses will give all purple while others will give purple and white in ratios 1:1, 3:5, or 1:3, although a frequent result will be a progeny of all white, which latter alone was expected under the conception that the purple color was due to the presence of a single gene. Although I have reared many families in which both parents were white, I have almost invariably obtained a progeny of all whites, but this is undoubtedly due to the fact that such crosses of white with white were nearly always made between sibs in wholly white-flowered families. Such crosses are necessarily homozygous with respect to the absence of one (or both) of the two genes whose joint action is necessary to the production of color. Crossing of white-flowered individuals of different parentage or of white sibs in hybrid families will doubtless quickly demonstrate the production of purple-flowered offspring by white-flowered parents, in the ratios required by theory.

Summary

The purple color in *Lychnis dioica* L. is a compound character, produced by the interaction of three distinct and independent genes in a manner exactly analogous to the similar colors in *Lathyrus, Matthiola,* etc.

The two types of purple color present in different individuals are a reddish and a more bluish-purple, the former being changed to blue by treatment with alkalies, and the latter changed to red by the addition of weak acids.

The bluish or alkaline color is hypostatic to the reddish or acid color, this being the reverse of the condition found in all other plants containing similar series of colors which have thus far been reported, unless possibly an isolated statement should prove correct that in *Primula Sinensis* "blue is hypostatic to all the red shades."

It is impossible to determine at present whether this reversal of the relation between bluish and reddish anthocyan results from the occurrence of positive characters for both alkalinity and acidity, or whether only one of these exists as a positive character and the alternative color is produced when this positive color-modifier is in the heterozygous state, the latter situation involving the dominance of absence over presence.

The rather wide fluctuation in the percentage of purple-flowered families resulting from the cross of heterozygous purple with white (*i. e.,* supposedly $DR \times R$), reported in a former paper, may have been due in part to the mixture of the ratios 3:1, 1:1, 3:5 and 1:3, all of which are expected Mendelian results, on the basis of present knowledge of the compound character of *Lychnis* colors.

Crosses between white-flowered plants should, not infrequently, result in progenies of all purple-flowered offspring or of purple and white in the ratios 1:1, 3:5, or 1:3. These results have not yet been found, owing no doubt to the fact that my crosses between white and white have been almost invariably made between sibs in wholly white-flowered families.

STATION FOR EXPERIMENTAL EVOLUTION,
COLD SPRING HARBOR, LONG ISLAND,
November 19, 1909.

LITERATURE CITED

1909. Bateson, W. Mendel's Principles of Heredity, pp. xiv + 396, 1909. Cambridge, University Press.

1902. Bateson, W., and Saunders, E. R. Experimental Studies in the Physiology of Heredity, I. Reports to the Evolution Committee of the Royal Society.

1905. Bateson, W., Saunders, E. R., and Punnett, R. C. Reports to the Evolution Committee of the Royal Society, II.

1906. Bateson, W., Saunders, E. R., and Punnett, R. C. Ibid., III.

1908. Baur, E. Einige Ergebnisse der experimentellen Vererbungslehre. *Beih. z. Med. Klinik.*, **4**: 265–292, 1909.

1908. Shull, G. H. Some New Cases of Mendelian Inheritance. *Bot. Gaz.*, **45**: 103–116, February, 1908.

1909. Shull, G. H. The "Presence and Absence" Hypothesis. *Amer. Nat.*, **43**: 410–419, July, 1909.

1901. Tschermak, E. Weitere Beiträge über Verschiedenwertigkeit der Merkmale bei Kreuzung von Erbsen und Bohnen. *Ber. Deutsch. Bot. Gesell.*, **19**: Heft 2, 1901.

1904. Tschermak, E. Weitere Kreuzungsstudien an Erbsen, Levkojen und Bohnen. *Zeitschr. f. d. landw. Versuchsw. in Oesterr.*, 1904.

1907. Wheldale, Miss M. On the Inheritance of Flower-color in Antirrhinum majus. *Proc. Roy. Soc.*, **79**: 1907.

1909. Wheldale, Miss M. On the Nature of Anthocyanin. *Proc. Cambridge Phil. Soc.*, **15** (pt. II.): 137–168, 1909.

IS REGENERATION A REPETITION OF THE ONTOGENETIC AND PHYLOGENETIC PROCESSES?

SERGIUS MORGULIS, A.M.

Facts are as unaffected and permanent as the universe. They are always present, whether we know them or not. Theories, on the contrary, are transitory conceptions, products of the intellect striving to comprehend the outer world. As a verbal expression of the unity underlying the overt diversity of phenomena and things, and as a mental picture of the connection between things, theories may be either perceived or imagined, a step towards absolute truth or a profound fallacy. Its fate depends wholly upon compliance with the facts, and it can not, therefore, be used as a *criterion of value* of the facts. Theories may ultimately be revised or discarded —facts remain forever.

With this commonplace in mind, we can clearly see that the question before us—namely, is regeneration a repetition of the processes of ontogeny and phylogeny?—is a matter of theory. As such, it is a much-debated subject which has been so often and so ably discussed in the past by several writers, that I should, perhaps, refrain from adding my quota to the dispute. But it has lately been called to my attention by an admirable monograph, by K. N. Davydoff.[1] As Davydoff writes in Russian, his work is practically inaccessible to American readers.

Considered from a purely technical standpoint, the monograph leaves little more to be desired. It is supplied with a large number of well-finished figures, and the text is lucid and concise. I should use only terms of praise if I were to speak on that score. I shall, however.

---

[1] K. N. Davydoff, "Observations on the Process of Regeneration in Enteropneusta," *Mem. de l'Académie Impériale d. Sc. de St.-Pétersbourg*, Vol. 22, No. 10, pp. 1–120, 1908 (Russian).

not concern myself with this side of the matter, as it is my prime object in the present article to scrutinize Davydoff's theoretical position.

On the very first pages Davydoff states the main article of his creed: that the fact that new organs, in the process of regeneration, originate from the same layers from which such organs originated embryologically proves that the two processes are parallel in cause. Since the hypothesis of the repetition of the phylogenetic processes in regeneration necessarily rests upon this assumption, as a major premise, it may be well, in the first instance, to examine closely its validity. This plan is preferable also because Davydoff himself in imparting his data and defending his thesis follows a similar course.

The reader is doubtless familiar with the way a comparison of the two-layered gastrula with an adult Cœlenterate had ultimately grown into Haeckel's celebrated ''Gastræa-theorie.'' This broad embryological conception, purporting to bind the entire animal kingdom with bonds of genetic relationship, postulates the homology of adult organs differentiated from similar germ-layers in the embryos. So fascinating was the application of this greatest biological generalization that the overweening confidence it bade became in time a source of grievous blunders. Contradictions have arisen on the ground of striking differences in the origin of organs in development and in budding, as was discovered to be the case in Bryozoa and in Tunicates. Likewise the discrepancy often observed between the methods of organ-formation in ontogeny and regeneration tended further to undermine credulity in the theory and the value of the germ-layers as a criterion of homology. Indeed, so seriously was this aspect of the theory threatened that conservative men, like L. Schultze, anxious to safeguard it from impending disrepute, were obliged to eliminate instances of budding and of regeneration from a consideration of homologies.

> . . . Die Entstehung eines Organs durch Regeneration oder Knospung keinen Anhaltspunkt giebt zur Beurteilung des Morphologischen Wertes seiner Entwicklung aus einem Keimblatt, d. h. die Verwertbarkeit der Keimblatt-Herkunft eines Organs für die Frage seiner Homologie mit einem anderen Organ, dessen Keimblattursprung ebenfalls bekannt ist, wird durch die Knospungs- und Regenerations-befunde in keiner Weise beeinträchtigt. (L. Schultze, p. 331.)

The inextricable contradictions which sprang from the tenets of historical and morphological significance of the germ-layers called forth even a more vigorous reaction. Braem subjected the theory to a thorough and relentless critique revealing its inadequacy. "Der Begriff Keimblatt," he proclaimed, "ist gar kein morphologischer sondern ein physiologischer Begriff. Keimblätter sind Organbildner." And further, he introduced the pragmatic principle that

> . . . Ein Schicht ist nicht deshalb Entoderm weil sie das innere Blatt einer Gastrula ist, sondern sie ist Entoderm weil sie den Darm bildet, weil sie die physiologische Charaktere des Darmblattes entweder bereits besitzt oder doch im Laufe der ferneren Entwicklung annimmt. . . . Massgebend ist nur die organbildende Potenz, die Funktion der zellschicht. (Braem, p. 431.)

While embryologists were thus questioning the importance of the germ-layer as a criterion and in fact were at a loss to know what was meant by a germ-layer, students of the histogenetic processes in regeneration were accumulating evidence to the effect that the new tissues generally arise from corresponding old tissues, and, consequently, from the same germ-layers from which those tissues had been differentiated in development. Although the evidence is based largely upon the investigation of the regenerative process in worms, the facts relating to this animal group as they are stated by various authors are too much at odds with each other to be of any real worth, at least so far as the problem of the relation between regeneration and ontogeny is concerned. This may seem a very strong statement, but it is justified by the frequent contradictions which one encounters in reviewing the literature. To be specific, I might mention the case of *Lumbriculus*. The histogenesis of the regenerated organs in this worm was studied very extensively by at least four investigators. There is scarcely a point of any importance upon which all are unanimously agreed. Unless one shares Davydoff's rosy optimism that "whatever is last is best," and that the latest contribution to the subject is necessarily the truest, the non-committal attitude of skepticism would seem far preferable.

Furthermore, the histological studies of the regenerative process have likewise revealed certain striking deviations from the usual course of things. Wolff's researches of the regeneration of the lens in salamanders showed that in regeneration the lens is formed by a method entirely different from that observed in embryonic development. In the embryo it arises as a thickening of the ectoderm covering the optic cup, while in regeneration—"Der Obere Irisrand ist nämlich offenbar die zweckmässigste stelle für die Enstehung der Linse."

Hazen discovered that in the anemone *Sagartia* the regeneration of the œsophagus involved some important departures from the ontogenetic process.

> In small pieces the œsophagus regenerates as an invagination of mesoglæa and endoderm in the shape of an inverted cup, in which the mesoglæa forms the middle layer, and which is covered on both outside and inside by entoderm. The ectoderm takes no part in the regeneration of the œsophagus.

Margaret Reed found that the muscles of a regenerating appendage in crustacea originate entirely from ectodermal cells. "When the first leg of the crayfish is thrown off at the breaking joint, no muscles are injured, and the muscles for the new leg are formed from cells proliferated by the ectoderm. In the hermit crab also the muscles of the new leg are formed by ectodermal cells." In ontogeny the muscles originate from endoderm.

The last discovery is of particular importance, not only on account of the different methods of muscle-formation in development and regeneration which it brought to light, but because it calls into question the conception of the determined specificity of tissues. And in point of fact, the problem of the relation between regeneration and ontogeny ultimately resolves itself into this wider problem of the specificity of tissues. In the crayfish and hermit crab cells, which under ordinary conditions of development never give rise to muscles, apparently have the potentiality to do so under certain circumstances.

The exceptional cases, alluded to above, are not of the kind that would tend to corroborate the rule. On the contrary, they tend to turn the whole question topsy-turvy. It rests with the adherents of the view that regeneration and ontogeny are parallel processes to bring forth a creditable explanation of these facts to fit them into their theory, for as long as they remain undisputed facts they must likewise remain the unapproachable stronghold of skepticism.

Davydoff in his recent monograph traced with great skill and painstaking care the history of each regenerating organ of *Ptychodera*. This laborious investigation led him to conclude that "the study of regeneration in *Enteropneusta* entirely corroborates the hypothesis that . . . all organs and tissues regenerate from elements of the same germ-layers from which they also developed in ontogeny" (p. 78).

This conclusion is adopted "even though at times there is no *complete* resemblance to the ontogenetic process" (*ibid.*).

The reservation is specially noteworthy since in another place we read the following:

> It must be pointed out that many departures from the general method of regeneration to be described further are of frequent occurrence; in fact, it might be said that each particular case presents some characteristic peculiarity: the details of the regenerative process vary indefinitely. . . . It is necessary, however, to account for all the conditions of each case in order to interpret any deviation from the typical; at present this is an impossible task. Only by making due allowance for

variations within the widest limits, it may be possible to delineate the normal course or type of regeneration (p. 16).

Without any intention on my part to detract from Davydoff's merits of having accurately ascertained the facts of the regeneration of *Enteropneusta,* it nevertheless seems to me that the manner of his argument is more entertaining than convincing.

Here, for instance, are samples of his reasoning. In *Ptychodera* (*Enteropneusta*) the new cœlome regenerates from elements of the old cœlome, *i. e.,* the new mesoderm arises from old mesoderm. So far, so good. Davydoff, however, is not fully satisfied with this achievement, as he is determined to prove to his reader that the parallelism between ontogeny and regeneration is of a far more subtle nature; but he encounters a stumbling block in that the cœlome in ontogeny arises as an evagination of the primitive endoderm. In the regeneration of the cœlome, however, the endoderm takes no direct part. Is that to be regarded as a discrepancy between ontogeny and regeneration? Sensible men might say that since the old cœlome had been differentiated from endoderm, therefore, the new cœlome regenerating from the old cœlome is likewise of endodermal origin, and would let the matter rest there. Davydoff is not contented with this sort of proof. He finds that in *Balanoglossus kowalewskii* the cœlome of the collar arises not as an independent outgrowth from the primitive gut, but is formed by proliferation of cells from the cœlomic pouches of the body. In other words, in *Balanoglossus kowalewskii* the cœlome of the collar originates not directly from the endoderm, but indirectly from the already differentiated cœlome of the body. Is not this a wonderful identity between the processes of regeneration and ontogeny in *Ptychodera* and *Balanoglossus?*

But how is it with the cœlome of the proboscis? In *Ptychodera* it regenerates by proliferation of cells from the cœlome of the collar. Does it arise in the same manner in the course of ontogeny? Davydoff appears a little embarrassed on this score. *Balanoglossus kowalewskii*, which served him such a good turn in his contention regarding the subtle similarity between the regeneration and development of the cœlome of the collar, is of no avail for the present purpose. In *Balanoglossus kowalewskii* the cœlome of the proboscis arises immediately from the primitive gut as an unpaired outgrowth. But what does it really matter how this end is accomplished in *Balanoglossus kowalewskii?* And why, proceeds Davydoff, should we be hasty in emphasizing too strongly this difference between ontogeny and regeneration, as long as we know absolutely nothing concerning the formation of the cœlome of the proboscis in the ontogeny of *Enteropneusta?*

Davydoff's criticisms, after the fashion of his argumentation, is superficial and unsubstantial. His criticism of Morgan misses the point completely. Attacking Morgan as the foremost leader of the opposite camp, and as one who gave the ablest expression to the skepticism concerning the supposed causal relation between processes of regeneration and ontogeny, Davydoff remarks:

> We must agree that Morgan's arguments as well as his whole critique are exceedingly weak. While referring in the literary index [Regeneration, 1907] to a number of works contradicting his views, he none the less makes no mention of them in the text, but exalts a few facts, which are in reality of no great significance, and often even count directly against Morgan's own contentions (p. 65).

This statement requires some comment, so unjustified does it appear to me. In the first place, that Morgan refers to works which take the other side in the disputed question is a good warrant that the question has not been considered one-sidedly. Davydoff, on the contrary, for some esoteric reasons and without any excuse whatever, closes his eyes upon the facts which challenge his hypothesis. Furthermore, Davydoff's allusion to the work of Abel, as one of a number of works supporting his assumptions, might likewise be questioned upon Abel's own authority. For Abel, enumerating the different ways of the regeneration of the end-gut, states definitely:

> Hinsichtlich des Verlaufs der Regeneration braucht jedoch durchaus keine mit den ontogenetischen Processen übereinstimmende Bildungsweise des Enddarmes stattzufinden.

In the second place, Davydoff's criticism is unjust because it arises from a lack of appreciation of the soundness of Morgan's skepticism. As a matter of fact, Morgan and his school do not *deny* that there is at times a very marked similarity between the methods of regeneration and ontogeny. Morgan is willing to go even further than that, and to admit a complete identity of the two processes. His position may be best formulated in his own apt words:

> The mistake, I think, is not in stating that the two processes are sometimes similar, or even identical, but *in stating the matter as though the regenerative process repeats the embryonic method of development*[2] (p. 213).

I dwell at such great length upon the question of the causal relation between regenerative and ontogenetic processes because, unless there is reasonable occasion for disbelieving it, the theory of the repetition of phylogenetic processes in the course of regeneration must not be dodged, as the next logical step. In the foregoing I have been emphasizing particularly the facts opposed to the theory not from any prejudiced neglect of the facts apparently favorable to the theory, but simply to show that the question of the connection between ontogeny and regeneration is far from being firmly established. To build upon this as a foundation elaborate theoretic superstructures is like erecting a magnificent edifice upon a foundation of quicksand.

But if regeneration repeats the ontogenetic process, as is claimed by some, what is the significance of the occasional departures of the end result of regeneration from that of normal development? The believers in the theory have a ready answer. Those are obviously cases of atavism, they say. Just as the connection between ontogeny and phylogeny is obscured by the cœnogenetic peculiarities of the former, so likewise the connection between ontogeny and regeneration is frequently obscured by the palingenetic peculiarities of the latter. To quote: "Die Uebereinstimmung (zwischen Regeneration und Embryonalentwicklung) bezieht sich gerade auf palingenetische züge, wärend cenogenetische viel leichter eliminiert werden" (E. Schultz). The application of the principle of atavism to phenomena of regeneration has been in vogue for nearly a quarter of a century, and Davydoff also records what he considers cases of atavism in the regeneration of Ptychodera, such as: the formation of two nephridial ducts instead of one; the failure to regenerate on the part of the ectodermal duct of the nephridium; the regeneration of a double instead of a single pericardial sac, etc.

---

[2] Italics are mine.

The novelty of Davydoff's work consists in the attempt to give to the principle of atavism practical application. If regeneration proceeds by more primitive methods, why not avail oneself of this opportunity to throw light upon such points of animal morphology as are obscured by the cœnogenetic methods of development? To Davydoff belongs the full credit for having ventured to accept this logical consequence of the preceding propositions. We shall return to this question later. At this moment I wish to examine the validity of the so-called "atavism" theory in regeneration.

The defects of this theory are twofold—the theory is not self-consistent, and, moreover, in the majority of cases it takes for granted what ought first to be proved. The inducement may be strong to interpret, for instance, the type of scaling on regenerating tails of lizards, totally different from the normal for the given genus and yet similar to that of another genus, as a "throwing back" to some common ancestral condition. The appearance of dorsal stripes on the regenerating tails instead of the usual annuli might with like justice be conceived as a "throwing back." But while maintaining the atavistic nature of the former, Boulenger finds no occasion for applying the theory to the latter case.

Barfurth finds that the axolotl often regenerates five fingers on an amputated limb. Considering the complexity of the regenerative mechanism, the frequent occurrence of abnormalities, and, as Barfurth himself points out, that "Modus und Product der Regeneration von der Art der Operation abhängig sind" it would seem that the regeneration of five fingers is of no more value from the point of view of the salamander's phylogeny than the double paw of a cat is for the appreciation of its phylogeny. Yet he is ready to believe that "die verhältnismässig häufige Regeneration einer fünffingerigen Hand beim Axolotl ist ein Rückschlag auf die ursprünglich normalerweise fünffingerige Hand der Amphibien."

It will, perhaps, not be devoid of interest to note that Ridewood, who studied the regeneration of the limb of the toad, expresses himself quite differently upon this question. "While in animals other than Anura," he says, "structural differences between the regenerated and the normal limb may be explained as phenomena of atavism, there is no evidence of such phylogenetic reversion in the regenerated limb-skeleton of the Anura under consideration."

It should be obvious that it is not sufficient to point to some abstract ancestor, an imaginary conception, but that the real ancestor must be known in order that the genuineness of the reversion may be established beyond doubt. It is absurd to apply the term "reversion" and "atavism" to sporadic growths, not represented in the normal development, of which the factors are, in most cases, entirely unknown to us.

The inconsistency ascribed to the theory may be further exemplified by the following instances. In tracheate insects, according to Brindley, the reproduced portion of an amputated appendage is invariably unlike the normal. In Blattidæ fewer than five tarsi regenerate, and the size of the parts is likewise different from the normal. Is the reduced number of tarsal joints in the regenerated appendages an indication of reversion to a more primitive condition? No advocate of the atavism theory would be likely to go so far as to oppose the authoritative opinion of entomologists which assumes the five-jointed condition as the primitive one. Yet even on its full face value this fact of dropping out of joints is in no sense different from the fact of the addition of an extra finger in the regenerating limb of a salamander which is professed to be a reversion. And, to be consistent, should we not also suppose on the basis of Herbst's discovery of the regeneration in crustacea of antennæ in place of extirpated eyes that the ancestors of these animals at the dawn of their history had no eyes, and that the antenna is the precursor of the eye?

One of the most amusing attempts to mould a regenerated structural peculiarity into the picturesque shape of an ancestral structure of overwhelming antiquity is that of Schimkewitsch, who very sagaciously interprets the regeneration of an amphibian lens in terms of atavism. As already mentioned in a previous section of the paper, the amphibian lens regenerates not from the skin but from the iris, which is a marked departure from the developmental process. This fact leads Schimkewitsch to suppose that the paired eyes of vertebrates must have primitively been similar to the epiphysis of reptiles, commonly known as the pineal organ or eye. This pineal organ possesses a lens-like structure which is formed by the thickening of the outer wall of the cup. The purely superficial resemblance of the lens regenerating from the iris of the eye and the lens-like thickening of the pineal organ is the starting point of Schimkewitsch's hypothesis. He says:

> Ursprünglich die paarigen Augen eine ebensolche Linse besassen wie wir sie im unpaaren Augen der Hatteria sehen, d. h. hervorgegangen aus der Wand der Augenblasse selbst.

It is needless to insist that, in the usual fashion, the author of the hypothesis is appealing for proof to a fantastic ancestral condition. But quite apart from that, the looseness of his argumentation is further increased by the circumstance that anatomists are by no means certain that the pineal body is an eye, and judging by the structure of its lens it may also be a heat-perceiving organ, as some indeed have suggested.

Thus far I have been considering what might properly be called the preliminary steps leading to the hypothesis, that the end result of regeneration differing from the usual result of ontogenetic development lends the key to a solution of obscure morphologic problems. This suggestion or idea is at the bottom of Davydoff's entire work; it persistently crops up here and there throughout the monograph. In short, it is the soul of that work.

From what has been said in the foregoing it ought to be clear that if the hypothesis of the repetition of ontogeny in regeneration, and also that of the atavistic nature of the deviations from the normal condition, are not false assumptions, they are at least deserving the verdict "not proven." Since in no known system of logic does the truth issue from propositions, either wholly untrue or else of such uncertain veracity as to leave free choice to intellectual likes and dislikes, it would seem that Davydoff was laboring largely under a mistaken principle.

I am, however, ready to go to the extent of granting, just for the sake of further argument, that the first two propositions are demonstrably true, and that consequently Davydoff's idea of using regenerated peculiarities for the purpose of solving obscure problems of phylogenetic importance is, humanly speaking, beyond objection. A moment's consideration will not fail to convince us that even though truth may be a quality of Davydoff's principle, its function could be either of purely negative value or even of no value.

The literature on regeneration abounds in instances of departures from the normal which appear either sporadically or even regularly in the course of regeneration of organs. Earthworms regenerate heteromorphic tails and planarians regenerate heteromorphic heads. Do these peculiarities signify any reversion to a more primitive condition? Double and multiple structures likewise frequently appear in the regeneration of organs, as, for instance, the regeneration of double heads in planarians or in *Lumbriculus*. Do these abnormalities bring any message about the normal state of things in the remote past? Likewise, as Davydoff informs us, *Enteropneusta* may regenerate double pericardial sacs or double notochords. What is the morphological and historical significance of these unusual formations? Going through a list of such irregularities and departures from the normal, one may doubtless find all gradations from the obvious freaks of nature down to such as may claim a respectable ''atavistic'' distinction. But the question is, what will guide us in discriminating between these various departures, for after all every departure in regeneration originates under the special conditions of an amputation. The manner in which Davydoff overcomes the difficulty of this question is both characteristic and interesting, and we shall return to it soon. It should be pointed out, however, first that no existing theory of phylogenetic significance can be invalidated to the slightest degree by the failure to regenerate on the part of such structural peculiarities or characteristics as may be postulated by the theory as primitive or ancestral. On the other hand, any sporadic growth in the process of regeneration, if by play of chance it should happen to coincide with a theoretical anticipation, would become an additional support to the theory. In other words, in any disputed theoretical problem of animal phylogeny the evidence derived from the study of regeneration must by the limitations of its own nature be always of the affirmative kind. It is the better part of wisdom to believe much too little rather than a little too much, and on this account we should hesitate to rely upon evidence from regeneration.

But to return to the original question as to what should guide us in deciding where, in regeneration, mere abnormalities or monstrosities end and where "palingenesis" and "atavisms" begin. Let us see how Davydoff proceeds with this question. He records among others two cases where occasionally double structures regenerate instead of the normally single structure, viz., the doubling of the pericardial sac and of the notochord. The meaning of these parallel facts is equally puzzling to us and, broadly considered, the two facts are to all intents and purposes of the same importance. But Davydoff rummages through the volumes in the library for light upon the significance of these extraordinary instances. There he discovers that the much-esteemed, and certainly authoritative writer of the "Beiträge zur einer Trophocœlthorie" in speaking of the "Herzblase" of *Balanoglossus* suggests in parentheses and under the auspices of a question mark that the "Herzblase" may have been primitively a double structure. This suggestion is expressed just in two words—(ursprünglich paarige?). Evidently Davydoff had not succeeded in finding in the literature another similar hypothesis that the notochord, too, may have been primitively a double structure. I judge so, because without offering any further reasons, he dismisses the puzzle of a double notochord by proclaiming it an abnormality, while honoring the double pericardial sac with the distinction of atavism.

Thus does Davydoff solve the question, and whatever merits or demerits his answer may have from the point of view of common sense, one thing is certain: that there is no direct, immediate way of deciding the question. We must fall back upon a theory, a hypothesis, a suggestion, even a mere guess, in distinguishing between what is abnormal and what is ancestral in regenerated structures. In a word, it is the theory which, in accordance with Davydoff's solution of the question, must give value to the observed facts.

This *principle* is diametrically opposite to the principle laid down in the introduction to this paper, that the nature of the relation between facts and theories is such that the facts can not be valued by their compliance with theories. We need theories for inspiration and enlightenment, we need facts to build upon; but to discriminate between facts in favor of any mental conception is to place oneself upon the inclined plane of immoderate speculation.

To sum up: While the evidence shows that as a rule organs originate from similar germ-layers, both in ontogeny and in regeneration, there are also some striking exceptions to the rule. The hypothesis, that the method of regeneration is causally influenced by the course of ontogeny, is, therefore, quite unnecessary as a corollary.

With the elimination of this hypothesis the conception of the atavistic nature of regenerated peculiarities, *i. e.*, the conception of a repetition in regeneration of phylogenetic processes, loses its chief logical support. This last theory, however, is also objectionable (1) because of its inherent inconsistency, (2) because it depends upon more or less problematic assumptions.

With both hypotheses, those of the repetition in regeneration of ontogenetic and of phylogenetic processes, now discredited, it would be venturesome to take sides in unsettled questions of animal morphology upon the ground of evidence deduced from a study of regeneration. But even if the hypothesis were correct, to accept it as a working principle is to put oneself deliberately into the logician's vicious circle—proving theories with facts approved of by the theories.

BIBLIOGRAPHY

Abel, M. Regenerationsvorgänge bei den limikolen Oligochaeten. *Zeitschr. f. wissenschaftl. Zool.*, Vol. 73, pp. 1–74, 1902.

Barfurth, D. Die experimentelle Regeneration überschüssiger Gliedmassentheile (Polydactylie) bei den Amphibien. *Arch. f. Entwicklungsm.*, Vol. 1, pp. 91–116, 1894.

Boulenger, G. A. (*a*) On the Scaling of the Reproduced Tail in Lizards. *Proc. Zool. Soc. London*, p. 351, 1888. (*b*) On an Iguana with Reproduced Tail. *Proc. Zool. Soc. London*, p. 466, 1891.

Braem, F. von. Was ist ein Keimblatt? *Biol. Centralbl.*, Vol. 15, pp. 427–443; 466–476; 491–506; 1905.

Hazen, H. P. Regeneration of the Œsophagus in the Anemone *Sagartia luciæ*. *Arch. f. Entw.*, Vol. 14, pp. 592–599, 1902.

Hepke, Paul. Ueber histo- und organo-genetische Vorgänge bei den Regenerationsprocessen der Naiden. *Zeitschr. f. wissenschaftl. Zool.*, Vol. 63, pp. 263–291, 1897.

Brindley, H. H. On Certain Characters of Reproduced Appendages in Arthropoda, particularly in the Blattidæ. *Proc. Zool. Soc. London*, pp. 924–958, 1898.

Davydoff, K. N. Observations on the Process of Regeneration in Enteropneusta. *Mem. de l'Académie Impériale des Sciences de St.-Pétersbourg*, Vol. 22, No. 10, pp. 1–120, 1908 (Russian).

Morgan, T. H. Regeneration, 1901.

Reed, M. The Regeneration of the First Leg of the Cray-fish. *Arch. f. Entwicklungsm.*, Vol. 18, pp. 307–317, 1904.

Ridewood, W. G. On the Skeleton of Regenerated Limbs of the Midwife-toad (*Alytes obstetricans*). *Proc. Zool. Soc. London*, pp. 101–106, 1897.

Schimkewitsch, W. Ueber den Atavistischen Charakter der Linsen regeneration bei Amphibien. *Anat. Anz.*, Vol. 21, No. 2, pp. 48–50, 1902.

Schultze, L. S. Die Regeneration des Ganglions von *Ciona intestinalis* L. und über das Verhältniss der Regeneration und Knospung zur Keimblätterlehre. *Jenaische Zeitschr. f. Naturwiss.*, Vol. 33, pp. 263–344, 1900.

Schultz, E. Ueber das Verhältniss der Regeneration zur Embryonalentwicklung und Knospung. *Biol. Centralbl.*, Vol. 22, pp. 360–368, 1902.

Wagner, F. von. Einige Bemerkungen über das Verhältniss von Ontogenie und Regeneration. *Biol. Centralbl.*, Vol. 13, pp. 287 296, 1893.

Wolff, G. Entwickelungsphysiologische studien I. Die Regeneration des Urodelenlinse. *Arch. f. Entwicklungsm.*, Vol. 1, pp. 380–390, 1895.

GENETICAL STUDIES ON ŒNOTHERA. I

Notes on the Behavior of Certain Hybrids of Œnothera in the First Generation

BRADLEY MOORE DAVIS

The following account is a report on the behavior in the first generation of the following sets of hybrids of *Œnothera* grown in the Harvard botanic garden in the summer of 1909: (1) *gigas* × *Lamarckiana,* (2) *muricata* × *gigas,* (3) *muricata* × *grandiflora,* (4) *biennis* × *grandiflora,* (5) *grandiflora* × *biennis.* The hybrids were not grown on an extensive scale, but represented rather a selection from the seedlings of the best plants in order to obtain for a special purpose the most vigorous crosses possible. The cross pollination was made in the writer's garden at Woods Hole in 1908, and the hybrids started in the hothouses at Cambridge early in January, 1909. Large rosettes were in most cases developed by the last of May, when the selected plants were set out in the botanic garden. All of the hybrids matured during the summer except a few plants of the cross *gigas* × *Lamarckiana,* which persisted in the rosette condition.

1. *gigas* × *Lamarckiana.* The parent forms of this cross were grown from seeds of De Vries, *Lamarckiana* having 14 chromosomes and *gigas* showing from a preliminary examination apparently twice this number. Twelve rosettes were planted exhibiting wide variation in the forms of the leaves, eight being similar to *Lamarckiana* and four similar to *gigas.* Two of the *Lamarckiana*-like rosettes and three of the *gigas*-like remained as rosettes throughout the summer, the former at the end of the summer being 3.5–3.7 dm. broad with leaves narrower than those of *gigas,* lanceolate and narrowly spatulate in form, the *gigas*-like being 4.5–5 dm. broad and indistinguishable from those of *gigas.*

Seven of the rosettes developed into mature plants which were similar to one another, 1–1.1 m. high with the characteristic habit and foliage of *gigas;* the large flowers and stout buds, ovaries and seed capsules, were also *gigas*-like. Some eighty attempts to obtain seed by guarded self pollination gave complete failures, which were the more interesting because ovaries presumably pollinated from neighboring *Œnotheras* by the numerous insect visitors matured large fruits and quantities of seeds; the failure to self-pollinate was thus apparently not due to abnormalities of the ovules. De Vries[1] reports that he has obtained fertile seed of this hybrid as well as of the reciprocal cross. There was a large proportion of abortive pollen, perhaps 80–90 per cent., but the remaining grains, as regards outward appearances, seemed normal. These latter consisted of a mixture of 3-lobed and 4-lobed grains in various proportions for different plants, the 3-lobed preponderating. Four-lobed pollen grains, as reported by Miss Lutz,[2] are characteristic of *gigas*.

2. *muricata* × *gigas*. The *gigas* parent furnishing the pollen of this cross was the same as in the preceding culture; the *muricata* parent was a wild plant from Woods Hole transplanted as a rosette to the garden of 1908. Hybrids of these were among the most interesting of the cultures of 1909. The well-developed rosettes were strikingly intermediate between those of the two parents, but fell clearly into two groups. Of the twelve plants in the culture six rosettes had leaves *muricata*-like in form but of a larger size than is typical of this species, and six rosettes had leaves broader than the above and conspicuously crinkled like the *gigas* parent.

The mature plants exhibited a similar difference; the first six had a habit and foliage that were *muricata*-like, the leaves, however, being longer and 2–3 times as broad; the other six plants presented a much stockier *gigas*-like habit with a stouter main stem and with leaves, which on the lower portion of the stem were strongly crinkled as in *gigas*. The flowers, inflorescences and capsules were quite similar in both groups of hybrids and presented forms and measurements intermediate between the two parents. The flowers, however, were decidedly smaller than the mean, and resembled those of the female *muricata* parent although about twice as large. The hybrids then as regards habit and foliage fell in about equal proportions into two groups, with greater resemblances to one or the other of the two parents. They presented an admirable illustration of the type of crosses called by De Vries[3] "twin hybrids", and reported for crosses between the *Onagra* group and *Lamarckiana*, or one of its derivatives, when these latter furnish the pollen.

---

[1] De Vries, H. ('08*b*), "Bastarde von Œnothera gigas," *Ber. deut. bot. Gesell.*, XXVIa, 754, 1908.

[2] Lutz, Anne M., "Notes on the First Generation Hybrid of *Œnothera lata* × *O. gigas*," *Science*, XXIX, 263, 1909.

These hybrids when self-pollinated set an abundance of seed which germinated readily, in sharp contrast to the experience recorded above for the hybrids of *gigas* × *Lamarckiana*. De Vries ('08*b*, p. 761) reports that hybrids of this cross as well as of the reciprocal have proved entirely sterile in his cultures. The fertility of my cross is especially interesting since we are dealing with a hybrid one of whose parents (*gigas*) has twice as many chromosomes as the other. A large proportion of the pollen grains, 75 per cent. or more, was abortive; the normal grains were almost wholly of the 3-lobed form (as in *muricata*), 4-lobed examples being uncommon.

3. *muricata* × *grandiflora*. There were two cultures of these hybrids based on two *muricata* parents from Woods Hole, pollinated, however, from the same *grandiflora* plant which was used in the crosses of *biennis* and *grandiflora*, a plant which is described somewhat fully below. The cultures comprised twenty-nine plants which did not pass through conspicuous rosette stages in the hot houses, but quickly developed the main stems, which were 1–2 dm. high when the plants were set out in the garden. Somewhat later these young plants with main stems 4–6 dm. high presented clearly a foliage intermediate between the parent types in form, color and texture. Thus the leaves were narrower, thicker, and a

---

[3] De Vries, H. ('07), "On Twin Hybrids," *Bot. Gaz.*, XLIV., 401, 1907. ('08*a*), "Ueber die Zwillingsbastarde von *Œnothera nanella*," *Ber. deut. bot. Gesell.*, XXVIa, 667, 1908.

darker green than those of *grandiflora,* but broader, thinner, and a lighter green than those of *muricata.*

On reaching maturity four plants exhibited flowers almost as large as those of *grandiflora,* and a habit and foliage more like this parent than was shown by the other hybrids; these four plants were, however, only 1.2 m. high while neighboring *grandifloras* were 1.5 m. high and much more extensively branched. The remaining hybrids, twenty-five in number, were strikingly *muricata*-like in habit and foliage except that the leaves were broader than those of that parent and the flowers more than twice as large, in size somewhat midway between the small flowers of *muricata* and the very large flowers of *grandiflora.* These hybrids then, as in the case of the *muricata* × *gigas,* fell into two groups (twin hybrids) with marked resemblances to one or the other of the parents, but with all structural characters blended. The proportion of four *grandiflora*-like to twenty-five *muricata*-like forms probably does not represent the normal ratio between the plants of these two groups which would be expected to appear in about equal numbers.

There was certainly no evidence from the cultures of any tendency on the part of the hybrids to resemble markedly the male parents (patroclinous) as was reported by De Vries ('07) to be the rule among *Œnothera* hybrids of the *Onagra* group. On the contrary five sixths of the hybrids were strikingly similar to the female parent, although, as stated above, it is not likely that these proportions represent normal ratios.

4. *biennis* × *grandiflora.* The parents of this cross were carefully selected with an end in view. The *biennis* plant was found wild at Woods Hole and transferred to the garden of 1908; it was chosen as representative of the broader-leaved types of this variable species with, however, only medium-sized flowers. This strain of *biennis* has proved constant in the cultures of 1909, presenting the characteristic *biennis* habit of a main stem about 1 m. high and long side branches arising from near the base of the plant. The *grandiflora* parent was one of nine plants grown from seed collected by S. M. Tracy

at Dixie Landing near Tensaw, Alabama, a well-known locality for the species. It was selected because of the breadth of the leaves, which in this species present a wide range of variation from lanceolate to broadly elliptical, and for the reddish coloration of the sepals which in other forms of *grandiflora* may be a clear green. This plant in the Woods Hole garden grew to be 2.1 m. high and presented a habit characterized by a strong main stem and long side branches rising from near its base.

Eight plants of this cross were brought to maturity in the garden of 1909 and exhibited a wide range of form. Seven of them were markedly *grandiflora*-like in habit and foliage, but with shorter main stems, 1.1–1.5 m. high; the flowers were somewhat smaller than those of the *grandiflora* parent. It is not safe, however, in a relatively small culture to draw conclusions from this large proportion of the hybrids resembling the male parent (patroclinous), especially since in the reciprocal cross described below approximately half of the plants resembled the female parent.

One of the hybrids (9*ba*) proved interesting for its resemblance in certain respects to *Œnothera Lamarckiana.* This plant was 1.3 m. high with a strong main stem and the side branches, as in *Lamarckiana,* well distributed along the axis, in contrast to the origin of the chief side branches from near the base of the plant which is generally characteristic of both *biennis* and *grandiflora.* The flowers were intermediate in their measurements between the *biennis* and *grandiflora* parents and so similar to those of *Lamarckiana* as to be practically indistinguishable in the features that would enter into a taxonomic description of the flowers of the latter. The differences (such as a slightly greater length of the stigma lobes) were probably no greater than would be found among the flowers of any culture of *Lamarckiana* which included a fair representation of the range of variation presented by this form.

The important differences between this hybrid plant and *Lamarckiana* were concerned then with the foliage, but were very marked. The leaves in general were *biennis*-like in form, but slightly larger in their measurements. Those on the lower portion of the main stem, which in *Lamarckiana* are 20 cm. or more in length and much crinkled, were in the hybrid only 11 cm. long and exhibited only a very slightly crinkled surface. The leaves along the upper portions of the branches and the bracts of the inflorescences were on the contrary larger than those of *Lamarckiana* and the inflorescence was, therefore, conspicuously larger leaved. The rosette condition of this plant, as grown in the hot house, was too transitory to give satisfactory conclusions as to what its characteristics would have been if given the opportunity of a more prolonged development.

This hybrid set seed abundantly when the flowers were self-pollinated. Less than 50 per cent. of the pollen was abortive. The normal grains were almost entirely 3-lobed like the pollen of the parents, but occasional 4-lobed grains were present.

5. *grandiflora* × *biennis*. The parents of this reciprocal cross were the same individual plants employed in the preceding (4). The culture consisted of twenty plants which fell clearly into two groups (twin hybrids) with greater resemblances to one or the other of the parent forms.

Nine of the hybrids were *grandiflora*-like in foliage and habit, the leaves being lanceolate in form, longer, narrower and more pointed than those of *biennis,* and the plants taller (1.3 m.), presenting also the numerous heavily flowered side shoots characteristic of *grandiflora.* The flowers were intermediate in form and measurements between those of the parent types, and essentially similar to the flowers of *Lamarckiana*. Five of these hybrids developed large rosettes with leaves similar in form to those of *biennis* but more pointed; the leaves of four of the rosettes exhibited marked crinkles like those of *Lamarckiana.*

The remainder of the hybrids of this cross resembled the *biennis* parent in foliage and habit. The leaves were broadly elliptical or ovate in form, shorter than those of the *grandiflora*-like hybrids, and thicker in texture. The plants were shorter (.8–1.1 m. high) and the habit *biennis*-like in being sparingly branched, the side branches arising from near the base of the plant and being almost as long as the main stem. The flowers were intermediate between the parent types, but exhibited a somewhat greater range of measurements than those of the *grandiflora*-like crosses.

In three of these *biennis*-like hybrids (*9ba, 9bb* and *9bc*) the flowers and inflorescences presented a structure so similar to that of *Lamarckiana* that they matched in all essentials the branches on certain *Lamarckiana* plants in the garden. The differences in the form of the bracts and parts of the flower were of the sort that can be observed in any reasonably large culture of *Lamarckiana.*

There were, however, striking differences between these three hybrid plants and *Lamarckiana* with respect to their foliage and habit of growth. The leaves on the lower portion of the stem were only 9–11 cm. long, about half the length of leaves similarly placed on *Lamarckiana,* and there were only slight traces of the crinkles so characteristic of *Lamarckiana.* The *biennis*-like habit of putting out long side branches from near the base of the plant was also very different from the usual habit of *Lamarckiana* in which the prominent side branches are more regularly distributed along the main stem.

These plants formed such transient rosettes in the hothouse that no conclusions could be drawn as to what would be their characters if allowed to develop more slowly. Seed was produced in abundance by self-pollinated flowers. Less than 50 per cent. of the pollen was abortive, the normal pollen, except for an occasional 4-lobed grain, was entirely 3-lobed.

GENERAL CONSIDERATIONS

While it is impossible to draw broad conclusions from these hybrids, which have as yet been observed only in the F_1 generation, a number of interesting points may be noted:

1. The characters of the parents, as presented in each

cross, were so blended that as regards the measurements of parts, habit, texture of foliage, etc., the average for each set of hybrids would probably present a fair mean between the two parents concerned. There was, however, a wide variation in the resemblance of the hybrids to one or the other of the parents.

2. No character of either parent was discovered which appeared as dominant in these hybrids of the F_1 generation, after the manner which has been described for certain forms (*e. g., Pisum*) that illustrate most conspicuously Mendelian dominance in the first generation.

3. Some of the hybrids of each cross presented a greater resemblance to one parent and some to the other, and the forms could therefore be arranged in two groups (twin hybrids) in one of which the maternal characters were most evident and in the other the paternal. There was no clear evidence that the hybrids of these cultures carried in marked preponderance the paternal characters (patroclinous), or on the other hand that maternal characters were more prominent. The range of variation among the hybrids was too great to permit of such conclusions.

It becomes a matter of interest to determine how plastic these hybrids will prove to be in later generations, and whether or not they will exhibit variations that may be fixed and accentuated by artificial selection. This line of enquiry will be especially pertinent to the behavior of those hybrid plants of *biennis* and *grandiflora* which in this F_1 generation presented *Lamarckiana*-like flowers and inflorescences, although differing markedly from *Lamarckiana* in habit and foliage.

I am greatly indebted to the Harvard botanic garden for the facilities placed at my disposal for this work.

Cambridge, Mass.,
December, 1909.

SHORTER ARTICLES AND DISCUSSION

THE MENDELIAN VIEW OF MELANIN FORMATION

Apparently there is no danger that the biological world will suffer permanent paralysis as the result of general acquiescence in hypotheses which have recently gained wide acceptance but for which fundamental proof seems not to be forthcoming. Especially is this the case when biologists whose special fields of work give them only an incidental interest in Mendelian and de Vriesian affairs will take the trouble to attach their batteries to the wires leading into the Mendelian field in order to counteract the paralyzing effect of what they regard as intellectual poison. I am a firm believer in the value of scientific trespass. Very frequently a group of scientists become moribund because they have no one to criticise them. An outsider who finds that his own work touches that of such a group may render real service by pointing out relations which those immediately concerned have overlooked and may thus cause readjustments of theory and hypothesis that are frequently much needed.

An excellent case of this kind is found in Riddle's interesting article in the *Biological Bulletin* for May, 1909.[1] One can hardly read this article without suspecting that Riddle is purposely somewhat extreme in his attack on the current interpretations of Mendelian phenomena in order to get a response from those who are responsible for these interpretations. It appears to the writer that Riddle attacks very successfully the de Vriesian interpretation of these phenomena. Unfortunately, however, he utterly confuses Mendelian facts with de Vriesian and Weismannian theories—hypotheses, rather, and attempts to throw both facts and hypotheses out of court. Riddle is not entirely to blame in this matter, however, for the de Vriesians generally have made the same mistake. If Riddle succeeds in arousing Mendelianists to a realization of the fact that the facts of Mendelian inheritance are not dependent on de Vriesian hypotheses he will have rendered a distinct service to biology.

---

[1] "Our Knowledge of Melanin Color Formation and Its Bearing on the Mendelian Description of Heredity," Oscar Riddle. *Biol. Bul.*, May, 1909, pp. 316–351.

Mr. Riddle must not forget that we have a long list of incontrovertible facts that are not in disagreement with the facts of melanin production cited by him, and which are not dependent on any theory involving discontinuous variation, but which may be interpreted in such a way as to take cognizance of the ascertained facts of physiological chemistry. Riddle throws all "factor" hypotheses overboard, apparently under the impression that they all depend on the Weismannian doctrine of determinants. Fortunately, such is not the case. These hereditary factors are established facts, while the Weismannian conception of them is, in the writer's view, probably wholly wrong.

Riddle points out that the chromogens in animals are tyrosin and related aromatic compounds. Tyrosinase, an oxidizing enzyme, converts tyrosin into melanins. Fuerth and Schneider concluded that "tyrosinase-like ferments are widely distributed in the animal organism and probably always appear wherever and whenever a physiological or pathological formation of melanin occurs." Gessard showed that the presence of acids, alkalis and salts has a marked effect on the colors produced by the action of tyrosinase on tyrosin. Bertrand determined the type of substance, of which there are many representatives, which tyrosinase can oxidize to melanins. In the oxidizing process each of these substances are converted step by step through a series of colors before reaching the final stage. They vary somewhat as to initial and final colors, the early stages being lighter than the later. The series of colors usually runs from yellow to orange, proceeding onward to brown or black. Any benzine nucleus with a hydroxyl attached can be converted to a melanin by tyrosinase. Some substances have red or mahogany as the final stage reached in the oxidation process.

Riddle further points out that the facts of the pathological development of melanins show the dependence of tyrosin oxidation upon somatic conditions which may be of temporary, intermittent, or reversible character, but he assumes, without sufficient basis, that these facts preclude the possibility of accounting for observed phenomena of color inheritance on a basis of specific transmission and segregation in the germ cells. He seems to think that any kind of segregation in the germ cells necessarily implies pangenes, such as those proposed by de Vries, or determinants, such as those proposed by Weismann. It is easily shown that this is not the case. The facts of segregation are not at all inconsistent with the idea that melanin formation is in itself a generalized function of the cell. Cytological investigations during the past two or three decades lend support to the hypothesis that the cell is composed of a number of more or less definite organisms. Now the production of black pigment, for instance, may be a process in which every organ of the cell plays a part. Riddle has shown that the particular color of an organism, when this color is melanic in character, is due to the fact that the oxidation process stops at a more or less definite point. We may imagine that the relative quantity of tyrosin and tyrosinase present in the cell has something to do with the point at which the process terminates under normal conditions. Now if a single cell organ should, because of some change in its nature, fail to produce its usual measure of one of these necessary substances, we may easily imagine that the point at which the oxidation process would stop would be changed accordingly. Now if the cell organ which is responsible for this difference happens to be a chromosome, and if chromosomes behave in the reduction division as a great many cytologists believe they do, then we at once get the phenomenon of Mendelian segregation independent of any idea of unit characters at all. This idea will be further developed in another paper by the present writer.

Riddle continually draws conclusions that do not seem to be justified by the facts he states. For instance, he states that melanin formations, under certain pathological conditions, "indicate that for the building of any melanin at all the actual conditions of the organism or the organ have a rôle to play that is quite out of keeping with any 'once-for-all determinance' by the shuffling of color factors through the germs." This is not a necessary conclusion unless we think of color factors as definite organs in the cell. I have just pointed out that what we have been calling factors may really be only differences in function of cell organs. There is no doubt at all that, for the development of almost any peculiarity or character, local conditions in the organism are important factors, but they are not the only factors. There must have come through the germ cell certain tendencies before these characters could develop at all. The horns of cattle are a good illustration of this point. These organs develop only at certain points of the organism, but the tendency to develop them when the proper conditions are given in the organism is unquestionably a matter of inheritance, nor can there be any question that there is a Mendelian segregation with reference to this tendency. This does not mean, however, that there is a bullet somewhere in the germ plasm which is wholly responsible for the development of horns. I imagine that the development of horn tissue is a process in which probably all of the organs of the cell participate; but if there is one organ which has become so changed in its functions that it can no longer take its usual and necessary part in the development of these organs, and if this organ is a chromosome, then we necessarily get the phenomenon of Mendelian segregation in inheritance with reference to this character.

Riddle points out a good many facts that it is well for Mendelianists to keep in mind in formulating hypotheses to account for the facts they discover. One of the most interesting of these is the finding by Spiegler that the hair of white horses and the wool of white sheep contain a white melanin. Some investigations indicate that these white melanins represent a more advanced stage of oxidation than do black melanins. White of this character we should therefore expect to be dominant, in the Mendelian sense. Riddle suggests that in certain white birds, and I presume the same would apply to albinos generally, the oxidation is not carried far enough to produce color. In these cases we should expect white to be recessive, in the Mendelian sense.

That melanin production is at least frequently the result of a long series of reactions is strongly indicated by Fornier's experiments on tadpoles. By giving varying amounts of nutriment he was able to produce a series of colors in these animals ranging from white through gray, and finally from yellow to black. Apparently these results were due to the fact that in individuals insufficiently nourished the oxidation process ended at different points in the series of possible stages.

The writer has observed a similar phenomenon in the case of cow-peas. In varieties of these plants having highly colored seeds it is a frequent occurrence to find imperfectly developed seeds of lower color than perfectly developed ones. For instance, the black-seeded varieties occasionally imperfect seeds are found which are light brown, due, presumably, to the fact that the oxidation process in these seeds did not reach the stage normally reached in perfect seeds. It may be further noted that in cow-peas melanin production seems to occur only in the later stages of development.

From a few facts like those above stated Riddle makes the sweeping conclusion that "in an animal that produces melanin color there exists all the machinery necessary to produce a series or scale of these colors. What is actually produced is, in several demonstrated instances, dependent on the physiological state of the organism." It does not necessarily follow that this is true in all organisms, or even in all animals, though it must be admitted that such may be the case. There is a good deal of evidence that in some organisms the oxidation processes do not lead through a series of colors, such as Fornier found in tadpoles, but that when color begins to appear at all it is of a definite character and that we have variation only in the amount of that color present. It seems quite probable that in some organisms the mechanism present is limited to the production of a single color character, yet this is a matter for further investigation.

Even if there is only one process of oxidation and the series of reactions results in a graduated series of color pigments this does not necessarily imply that a tendency to a certain color is not purely hereditary and that it could not undergo the phenomena of segregation. The normal stage of oxidation reached in an organism may be an intermediate one, as in red cattle. If a single cell organ is responsible for the oxidation process stopping at this stage, and if that cell organ behaves as chromosomes appear to do at least in some organisms, then we would necessarily have the phenomenon of Mendelian segregation.

Riddle seems to labor under the impression that in order to explain the so-called Mendelian factors it is necessary to assume an indefinite number of specific enzymes or chromogens. I think I have already said enough to point out that this is not the fact. There is much evidence, however, that in the color of animals we do have at least three specific enzymes or chromogens, for we find three kinds of color material deposited in the same parts of the organism. Furthermore, the tendency to produce each of these three types of pigments has been demonstrated to be separately heritable.

Riddle points out the very interesting fact that Miss Durham[2] investigated the enzymes in the skin of black, chocolate, yellow, and albino mice, and reported finding enzymes for black, chocolate, and yellow. Riddle criticizes Miss Durham's conclusions for no other apparent reason than that they apparently oppose his views. In albinos Miss Durham was not able to decide definitely concerning the presence of enzymes but was of the opinion that the enzymes were not present. Riddle's suggestion that yellow is a blend between albino and black would be quite interesting if we did not know that it is not true. Castle has recently shown that the tendency to produce yellow pigment, in rabbits at least, is a separately heritable tendency. On the other hand, we can agree with Riddle's statement that the "data warrant the definite statement that yellow mice are forms with the power of oxidizing tyrosin compounds, to an intermediate point."

---

[2] *Proceedings Royal Society,* Vol. 74.

If it were not for the well-established facts of segregation in the inheritance of color, Riddle's statement that "in gametic unions we deal not at all with factor particles but merely mix and amalgamate to various degrees powers of tyrosin oxidation and conditions supplied by the differentiations of tissues and organs, together with environmental conditions external and internal, supply whatever else is concerned in color production." It is really to be regretted that Riddle does not know more of the facts of color inheritance, for his incisive remarks indicate that if he knew these facts and took proper cognizance of them he would be highly useful to Mendelianists by way of developing an explanation of Mendelian phenomena more in keeping with the facts of physiological chemistry.

His criticism of Castle's work on rabbits is entirely unfounded. He assumes that the factors found by Castle can not exist apart from pangenes of the de Vriesian type, each of which is wholly responsible for the development of a Mendelian character. Castle's work shows that he has no such idea. He merely worked out the facts of color inheritance in rabbits, and, except for a brief reference in his closing paragraph about a possible mechanism for their explanation, gives no indication that he has any theory to explain them. He certainly does not commit himself to the de Vriesian theory. Castle has shown us that there are three kinds of pigments in the hairs of rabbits whether they should be there or not, and that the tendency, under normal conditions, to produce these pigments is hereditary; furthermore, that these tendencies are separately and independently transmitted. The fact is that there is nothing in the scheme of color factors presented by Castle inconsistent with the facts of color production presented by Riddle, unless it be that they call for two or three more or less distinct oxidizing processes instead of only one. Even the view that there is only a single process involved is not excluded if we can find a mechanism operative in development that stops the oxidation partly at one stage and partly at another.

I agree with Riddle that the placing of the "uniformity-spotted," etc., factors on the part of Castle in the germs of rabbits as alternative factors is a virtual surrender of the whole theory of discontinuous variation. According to my view, this theory has never had any sound basis except as a result of irregularities in the behavior of chromosomes, and Mendelian facts are not dependent on any such theory or in any way related to it, as the writer has repeatedly pointed out. Professor S. J. Holmes has also pointed out the fallacy in the assumption that Mendelian phenomena necessarily prove the theory of discontinuous variation.

That there may be more than one oxidation process concerned in the development of color in organisms is shown by a number of facts cited by Riddle. He gives a table of oxidation processes in which the end reactions result in various colors. He further cites the fact that lipochromes and guanin may possibly be the source of color in certain amphibia.

The author attempts to explain the variability in the second generation of hybrids as a result of unstable equilibrium of oxidation processes in the first generation. According to his view each of the gametes represents a stable condition. The first generation may be a compromise between the stable conditions found in the two gametes. In the second generation there is a tendency to revert to one or both of the stable points. This view is hardly in keeping with observed phenomena. The regularity with which certain types appear and their subsequent behavior with reference to the transmission of hereditary tendencies indicate, apparently beyond question, that there is some such definite segregation as would result from the assumption that the chromosomes play an important part in the general processes of cell metabolism.

Riddle shows his lack of knowledge of Mendelian principles and facts in his reference to the real contributions which Mendel has made. "The really important Mendelian contribution being that certain definite characters (such as have according to my belief, rather general processes as a basis) of different races may be combined to form new fixed races" (with which we all agree). "The establishment of this last fact has been most commonly considered by Mendelians on the one hand a consequence of the laws of dominance (!) and segregation, and on the other hand as a strong argument for a 'representative particle' basis for these two sets of phenomena." There are some Mendelians who really do not believe there is any law of dominance, and there are many more Mendelians who do not believe in a representative particle theory at all. Here, as elsewhere throughout his paper, Riddle confuses Mendelism with de Vriesianism and Weismannism. The following quotation applies only to de Vriesians and Weismannians, not to Mendelians: "With an eye seeing only *particles* and a speech only symbolizing them there is no such a thing as the study of a *process* possible." Castle in his work on rabbits has no such particles in his mind's eye; his terminology does not imply them; he merely describes the facts of color inheritance.

While in this review of Riddle's most interesting paper the writer has been compelled to appear to combat him at almost every point, he is quite in sympathy with Riddle's point of view. The thing he has tried to combat is Riddle's confusion of Mendelian facts with de Vriesian hypotheses. The writer hopes in the near future to be able to present a theory of Mendelian inheritance which is independent of the idea of unit characters and wholly independent of the idea of discontinuous variation.

W. J. Spillman.

NOTES AND LITERATURE

Seton's "Life Histories of Northern Animals."[1]—Mr. Seton is widely known to the general public as a lecturer on wild animals and as the author of several popular works on the same subject, of which his "Wild Animals I have Known" is the type, wherein the life of the species is personified in the history of an individual representative, as in "Lobo, the King of Currumpaw," "Silverspot, the Story of a Crow," "Raggylug, the Story of a Cottontail Rabbit," "The Winnipeg Wolf" and others. To his fellow specialists he is also known as a naturalist of wide experience with bird and mammal life, a serious, conscientious and zealous field observer, and the author of a number of strictly scientific papers on the mammals and birds of Manitoba and other parts of Canada.

His equipment for the present undertaking is exceptional; in addition to ability to express forcibly and concisely the results of his observations, he has rare artistic talent, and a field experience of some thirty years, covering widely separated districts in the United States and Canada. His sketches from life of the poses of animals, his diagrams and plans of the underground habitations of burrowing species, his delineations of tracks, of dens and other habitations, and of structural characters, in addition to his excellent plates of the animals themselves, lend greatly to the value and interest of the text.

In the present work the popular writer's license is laid aside for the plain every-day narrative of actual fact. As he states in his preface, "This aims to be a book of popular Natural History on a strictly scientific basis." Again he says: "As this is a book of Life histories or habits, I have occupied myself as little as possible with anatomy, and have given only so much description of each animal as is necessary for identification. My theme is *the living animal.*"

---

[1] "Life Histories of Northern Animals: An Account of the Mammals of Manitoba." By Ernest Thompson Seton, Naturalist to the Government of Manitoba. With 68 maps and 560 drawings by the author. Published by Charles Scribner's Sons, New York City, 1909. 2 vols., roy. 8vo. Vol. I, Grass-eaters, pp. i–xxx, 1–673, pls. i–xlvi, text illustrations 1–182 (many full-page), and maps 1–38. Vol. II, Flesh-eaters, pp. i–xii, 675–1267, pls. xlvii–c, text illustrations 183–207 (many full-page), and maps 39–68. $18.00 net per set.

We have here, in the author's own words, the scope and purpose of the work, which is restricted to the sixty species of mammals found in the province of Manitoba. They chance to include, however, most of the game and fur-bearing animals of North America, and these have been followed into such varied environments as the Barren Grounds of northern Canada, the heavily forested districts to the southward, the Rocky Mountains, the Great Plains region, and the arid southwest.

The introductory matter deals with the physical features of Manitoba, the life-zones and faunal areas of North America (illustrated with a full-page map), and with the general plan adopted in treating the species. The descriptions of the animals are brief but diagnostic, and with the accompanying illustrations serve to give one a fair impression of the species as seen in life. The incidents of its history are set off by side headings, which are numerous, and vary in accordance with the diverse traits of different species; all are defined in the introduction, which fully connotes the author's view-point in preparing these life histories. The geographical range of each species is shown by means of maps, based on patient research and indicating present knowledge of the subject.

Mr. Seton's "Life Histories" should be of interest not only to the naturalist, to the woodsman and to the general reader, but to those interested in the psychology of animals. Mr. Seton thinks that "no one who believes in evolution can doubt that man's mind, as well as his body, had its origin in the animals below him"; and with this thought in view he has sought "among these our lesser brethren for evidences of it—in the rudiments of speech, sign-language, musical sense, esthetics, amusements, home-making, social system, sanitation, wed-law, etc." But he adds: "As much as possible, I have kept my theories apart from my facts, in order that the reader may judge the former for himself."

His method of treatment may be illustrated by reference to his account of the gray wolf, to which animal forty pages are given. These include, besides the text, comparative characteristic outlines of gray wolf, coyote and fox as seen at a distance; a full-page plate of the animal from a drawing from life; a full-page map of the range of North American wolves; a full-page plate of life studies of wolves (head-pieces); a full-page plate of a gray wolf scratching himself (four figures); full-page plate of gray wolf approaching to attack; photographs of Lobo in a trap (half-tone plate, two views); tracks of large gray wolf (full-page illustration); the grayhound that followed too far (full-page plate of wolf and dog); "blood on the trail" (full-page study from life); and tail-piece; all (except the half-tone plate) from drawings by the author. The text gives the gray wolf's technical and vernacular names, its external characters and its life history; the latter under the side-headings: range, individual range, abundance, sociability, mating, life-long union, den, gestation, young, maternal instinct, growth of young, feeding young, enemies, education, history, habits, never attack man, fishing, food, moose-killer, storage, property instinct, doping, voice, intercommunication, smell-power, odor-glands, wolf telephones, registering, expression of scorn, expression of anger, some remarkable wolves, courage of wolves, chivalry, speed, track, strength, swimming, social amusements, sanitation, hybridity, as training-dogs, dogginess, latent ferocity, diseases, wolf-killing, poisoning, trapping, fur. The other species are treated with similar detail, but the points especially considered vary, of course, with the traits and distinctive haunts and manner of life of different species.

The heading "never attack man" is somewhat modified in the context, for he says:

> Their extreme shyness is partly a modern development, as also is the respect for man, which now possesses every gray wolf in the cattle country. There are many records that show the wolf to have been a continual danger to man in the bow-and-arrow days. There can be no doubt that then man was considered a fair prey, . . . a creature to be eaten in times of scarcity. Consequently, each winter in America, as in Europe, a number of human beings were killed and devoured by hungry wolves. . . . Man with the modern gun is a different creature from man with the bow and arrow. The wolves have learned this, and are now no more a menace to human life than are the prairie wolves or coyotes. Not only do they abstain from harming man, but they have learned that they are likely to be harmed by him, unless they keep out of sight in the daytime. . . .
>
> In accounting for these changes it is not necessary to attribute human intelligence to this animal. Evidently much hard luck and many unpleasant surprises have engendered in it a deep and general distrust of things strange, as well as a well-founded fear of anything that bears

> a human taint. This distrust, combined with its exquisite sense of smell, may explain much that looks like profound sagacity in this animal. Nevertheless, this will not explain all. . . .
>
> And even ascribing much to mere shyness does not remove it from the sphere of intelligence, though doubtless ranking it lower in that department, making it a vague fear of the unknown, in place of a dread of danger well comprehended.

Space does not permit further illustration of the author's manner of treatment, as illustrated in the history of the otter, fox, beaver and of many of the burrowing species. It must suffice to say that the amount of new information about the habits of North American mammals set down in these two volumes is surprising, with which is woven the best that has been contributed by previous observers. No work of like character, it is safe to say, has ever before been attempted, and doubtless many years will pass before another like it is given to the public. No such persistent, prying, friendly interest has before been shown by any student of wild mammals, whose life secrets are so much more difficult to fathom than those of birds or insects, owing to the nocturnal habits or shyness and secretiveness of most of the species, and the semi-subterranean manner of living of nearly all of the smaller forms; the squirrels and some of the larger herbivores are almost the only species open to every-day observation.

J. A. Allen.

American Museum of Natural History,
New York.

DO PARTHENOGENETIC EGGS OF HYMENOPTERA PRODUCE ONLY MALES?

In view of the simple relation found to exist in the bee between the fertilization of the egg and the sex of the individual, other hymenoptera have presented considerable difficulties. Recent evidence indicates that unfertilized eggs of ants may produce both sexes, and some species of saw-flies produce chiefly females, others chiefly males, from unfertilized eggs. Two recent papers report the results of experiments with parthenogenetic eggs of *Lysiphlebus tritici*, which is parasitic on the grain aphis, *Toxoptera graminum*. The first of these is entitled "Investigations of *Toxoptera graminum* and its Parasites," by

F. M. Webster, in the *Annals of the Entomological Society of America,* for June, 1909. Previous experiments with lysiphlebus had indicated that parthenogenetic eggs invariably gave rise to males. Webster and his assistants, however, report varying results. Females of lysiphlebus, reared in isolation to prevent fertilization, were placed with toxoptera which had been raised under cover to preclude previous parasitism. Of 48 such females, 44 produced only males; the other four produced females also. The few females from these last four parents were allowed to lay eggs under the same conditions; two of the families gave only males, the other two again produced some females. In the third generation one of these two families ran all to males, and in the fourth generation the remaining family gave only males.

Similar evidence is given by S. J. Hunter in "The Green Bug and its Enemies," *Bulletin of the University of Kansas,* Vol. IX., No. 2, October, 1909. The experiments were carried out by P. A. Glenn and Miss McDaniels, and the usual precautions were taken to prevent fertilization of lysiphlebus and parasitism of the aphids. While some families included only males, others had a small percentage of females. Of an aggregate of 352 individuals reared from parthenogenetic eggs, 339 were males, 13 females. Later generations seem not to have been bred from any of these females. Among other individuals from parents which may or may not have been fertilized, 34.5 per cent. were males.

A. FRANKLIN SHULL.

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE AUGUST NUMBER

The New Flora of Krakatau. Professor DOUGLAS HOUGHTON CAMPBELL.

A Male Crayfish with Some Female Organs. Professor E. A. ANDREWS.

Present Problems in Plant Ecology:

Problems of Local Distribution on Arid Regions. Professor VOLNEY M. SPAULDING.

The Relation of the Climatic Factors to Vegetation. Professor EDGAR N. TRANSEAU.

Notes and Literature: Recent Experiments on the Inheritance of Coat Colors in Mice, Professor T. H. MORGAN. Some Experiments in Breeding Slugs. Professor T. D. A. COCKERELL.

CONTENTS OF SEPTEMBER NUMBER

On an Early Tertiary Land-connection between North and South America. Dr. R. F. SCHARF.

Notes on the Relations of the Molluscan Fauna of the Peruvian Zoological Province. Dr. WILLIAM HEALEY DALL.

Remarkable Development of Starfishes on the Northwest American Coast; Hybridism; Multiplicity of Rays; Teratology; Problems in Evolution; Geographical Distribution: Professor A. E. VERRILL.

Shorter Articles and Correspondence: Is there a Selective Elimination of Ovaries in the Fruiting of the Leguminosæ: Dr. R. HARRIS.

Notes and Literature: *Ichthyology*—Ichthyological Notes, President DAVID STARR JORDAN. *Parasitology*—Professor H. B. WARD. *Plant Cytology*—The Permanence of Chromosomes in Plant Cells, Dr. BRADLEY M. DAVIS.

CONTENTS OF THE OCTOBER NUMBER

The Non-muscular Articulations of Crinoids. AUSTIN HOBART CLARK

On Some Dinichthyid Armor Plates from the Marcellus Shale. BURNETT SMITH

Are Species Realities or Concepts only. Professor J. H. POWERS.

Shorter Articles and Discussion: A Light Weight, Portable Outfit for the Study and Transportation of Ants. EDITH N. BUCKINGHAM. Comparison of Cænolestes with Polyprotodonta and Diprotodonta. PAULINE H. DEDERER.

Notes and Literature: *Comparative Psycholoy*—Bohn's "The Birth of Intelligence": Professor H. S. JENNINGS. *Mammalogy*—Osgood's Revision of the Mice of the Genus Peromyscus, Dr. J. A. ALLEN, LEO ERRARA, Professor CHARLES E. BESSEY.

CONTENTS OF THE NOVEMBER NUMBER

The American Toad (Bufo lentiginosus americanus LeConte). NEWTON MILLER.

Notes on the Behavior of the Domestic Fowl. PHILIP B. HADLEY.

Vitality of Pine Seeds and the Delayed Opening of Cones. Professor W. C. COKER.

The Affinities of the Echinoidea. AUSTIN HOBART CLARK.

The Early Breeding Habits of Amblystoma punctatum

Notes and Literature: *Marine Biology*—Papers from the Tortugas Laboratory, Professor WILLIAM E. RITTER. *Experimental Evolution*—Inheritance of Color in Pigeons, R. B. HORTON.

CONTENTS OF THE DECEMBER NUMBER

The Cuticula and Subcuticula of the Trematodes and Cestodes. Professor HENRY S. PRATT.

The American Toad (Bufo lentiginosus americanus, LeConte). NEWTON MILLER.

Observations on Copulation among Crawfishes with Special Reference to Sex Recognition. Dr. A. S. PEARSE.

Shorter Articles and Correspondence: Degeneration accompanying Inbreeding. Professor C. B. DAVENPORT. A Note of the Prairie-dog Owl which Resembles the Rattlesnake's Rattle: Dr. J. ARTHUR HARRIS.

Notes and Literature: The Causation of Sex, Professor H. E. JORDAN.

Index to Volume XLIII.

CONTENTS OF THE JANUARY NUMBER

The Reappearance in the Offspring of artificially produced Parental Modifications. Dr. FRANCIS B. SUMNER.

A Bimodal Variation Polygon in Syndesmon thalictroides and its Morphological Significance. Dr. J. ARTHUR HARRIS.

The Miocene Trees of the Rocky Mountains. Professor T. D. A. COCKERELL.

A Suggestion regarding Heavy and Light Seed Grain. L. R. WALDRON.

Notes and Literature: *Mammalogy*—Nelson's Monograph of the North American Leporidæ, Dr. J. A. ALLEN. *Neurology*—Edinger's Vorlesungen über den Bau der nervösen Centralorgane, Professor G. H. PARKER.

Single Number 35 Cents

Yearly Subscription, $4.00

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y.

Sub-Station 84: NEW YORK

Lancaster, Pa.

Methods in Plant Histology

By CHARLES J. CHAMBERLAIN,

Second edition, revised and much enlarged; 272 pages, with 88 illustrations, 8vo, cloth; net $2.25, postpaid $2.39

THE first complete manual to be published on the subject of botanical microtechnique. It contains detailed directions for collecting and preparing plant material for microscopic investigation, setting forth the advantages and disadvantages of the different methods.

Will no doubt find a place in every well-regulated library, and will be found very useful by private students.—*Plant World.*

It is an excellent book for the individual worker and for classes in colleges.—*Education.*

A Laboratory Guide in Bacteriology

By PAUL G. HEINEMANN,

158 pages, interleaved, with 37 illustrations, 12mo, cloth; net $1.50, postpaid $1.61

A CLEAR and concise presentation of bacteriological technique, designed principally as a manual for the medical student, but highly useful also as a reference book for the biological teacher and investigator, as well as for practical workers in the fields of medicine and hygiene.

The instruction given is clear and accurate, and the practical exercises are well selected.—*The Lancet* (London).

A book such as this must facilitate very greatly the practical class work, for which it is most excellently adapted. — *American Journal of Medical Sciences.*

The directions are clear and concise, and every stage is described so carefully that it is hard to see how the student can go astray. Physicians who are rusty in bacteriology cannot do better than buy this little book. The book is beautifully printed and bound.—*American Journal of Clinical Medicine.*

Animal Micrology:

Practical Exercises in Microscopical Methods

By MICHAEL F. GUYER,

250 pages, 8vo, cloth; net $1.75, postpaid $1.88

THE title of this book will explain its scope. It is intended as a laboratory manual for textbook use. Its aim is to introduce the student to the technique of microscopic anatomy and embryology, emphasizing details of procedure rather than descriptions of reagents or apparatus. Sufficient account of the theoretical side of microscopy is given to enable the student to get satisfactory results from his microscope.

The directions are simple, explicit, and complete.—*American Journal of Clinical Medicine.*

The medical student will find it very useful as a guide to microscopic work.—*Journal of the American Medical Association.*

This is one of the cleanest works on microscopical technique we have ever seen, and is especially suitable for the beginner. It is full of points, tricks of technique not mentioned in other works, and is one that every student and physician should have.—*Medical Century.*

This valuable book is strong through its rigid exclusion of the trite and the conflicting. It is lucid and helpful, because a man long practiced in practical work has given what he believes the most expeditious and reliable method of obtaining a definite and comprehensive result. — *Medical Notes and Queries.*

A concise, eminently practical, and well-classified treatment.—*Science.*

The expositions of the methods recommended are admirably clear.—*Nature.*

One of the best and most practical works upon microscopic technique with which we are acquainted.—*American Naturalist.*

As a textbook it can hardly be improved. The research worker will find in this book just the information he frequently needs in preparing material with which he is not familiar.—*School Review.*

It does present in very clear form a judicious selection of methods, including an excellent untechnical account of the microscope and its optical principles, adequate for the undergraduate course in histology.—*Journal of Comparative Neurology and Psychology.*

ADDRESS DEPT. 64

Chicago THE UNIVERSITY OF CHICAGO PRESS New York

VOL. XLIV, NO. 519 MARCH, 1910

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. The Imperfection of Dominance and Some of its Consequences. Dr. C. B. DAVENPORT 129

II. Experimental Evidence on the Effectiveness of Selection. Professor H. S. JENNINGS 136

III. The Artificial Production of the Parthenogenetic and Sexual Phases of the Life Cycle of Hydatina senta. A. FRANKLIN SHULL 146

IV. The Significance of the Courtship and Secondary Sexual Characters of Araneads. Professor THOS. H. MONTGOMERY, Jr. 151

V. Notes and Literature: Notes on Ichthyology, President DAVID STARR JORDAN. A New Catalogue of Hemipterous Insects, Professor T. D. A. COCKERELL . 178

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS
Lancaster, Pa. Garrison, N. Y.
NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

TO ORNITHOLOGISTS AND MUSEUMS

W. F. H. ROSENBERG
Importer of Exotic Zoological Specimens
57 Haverstock Hill, N.W., England

Begs to announce the publication of a new Price List (No. 11) of Bird Skins. This catalogue contains over 5,000 species, and is the largest and most complete price list of birds ever published. It is arranged in systematic order, based on the classification of the British Museum "Catalogue of Birds," with authors' names, indications of localities, and an index to families. It will be sent gratis and post free on application, as will the following lists:
No. 7, Mammals; No. 8, Birds' Eggs;
No. 9, Reptiles, Amphibia, and Fishes.

Largest stock in the world of specimens in all branches of Zoology.

Specimens sent on approval.

Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

Henry Holt & Company
34 West 33d St., New York
378 Wabash Ave., Chicago

Microscopes and Accessories
Hand Cameras of Highest Quality
Binoculars, Prism and Galilean
the best obtainable for Nature Study
Scientific Instruments
Laboratory Apparatus
Max Meyer 18 West 27th St. New York
"Quality, Prices, Service Right."

THE
AMERICAN NATURALIST

Vol. XLIV *March, 1910* No. 519

THE IMPERFECTION OF DOMINANCE AND SOME OF ITS CONSEQUENCES[1]

DR. C. B. DAVENPORT

Station for Experimental Evolution, Cold Spring Harbor, N. Y.

It has long been recognized that in Mendelian heredity dominance is frequently imperfect. Mendel himself appreciated this fact, for he defines dominant characters as those "which are transmitted entire, or almost unchanged, in the hybridization" and points out that the hybrids between purple-red flowered and white flowered peas have lighter flowers than the darker parent. Indeed, in his letters to Nägeli he speaks of the *hybrid-form* of a character, recognizing that the hybrid character is not always that of one parent. Practically all hybridizers of the last nine years, and especially Correns and Bateson, have observed and laid emphasis on this imperfection of dominance. I can only add my testimony to theirs. It will be well to illustrate the general principle by some concrete examples. Bateson, and later Baur, found in hybrids between the prickly and non-prickly capsuled Datura that the prickles were much reduced in size. Correns found the hybrids between green- and yellow-leaved Mirabilis to have light green leaves; and in the same plant, variegation, though recessive, may be detected in the heterozygotes. Further, Mirabilis typica, 90 cm.

---

[1] A paper read before the American Society of Naturalists, December 29, 1909.

tall, crossed with *nana*, 40 cm. tall, produces offspring of 70 to 85 cm., thus failing to attain the dominant stature. Shull finds, in Shepard's purse, the heterozygote between elongated and non-elongated primary lobe to be imperfectly elongated, and the same investigator has devised a neat chemical experiment illustrating imperfect dominance. Morgan states that in hybrids between gray and albino rats, gray fails on the belly. In Lang's snails uniform shell color dominated over bands, but the hybrid shows pale bands. In poultry, extra toe dominates imperfectly over normal toe; complete inhibition of shank feathering dominates imperfectly over non-inhibition, so that some feathers appear; median comb dominates over absence so imperfectly that it is much reduced in the hybrids; dominant whites crossed with black give speckled females. Thus, the discoverer of dominance and his followers have generally recognized and laid emphasis on its imperfection; and were it not for certain careless exponents of Mendelism and a human tendency to substitute a skeleton formula for the living truth this introduction might have been spared.

Of imperfection of dominance there are all degrees, as Correns pointed out in 1905. The extreme case is complete failure to dominate; it has been observed many times. Thus Lock found that while black maize dominates over white, whites are in excess of expectation in subsequent generations and some of them prove to be heterozygous. Lang found hybrids between red and yellow snails to give exceptionally the recessive yellow. In poultry, median comb crossed with no median will give no median in 5 to 10 per cent. of the offspring. Extra toed crossed with normal poultry give over 20 per cent. of the recessive normal-toed type. The inhibitor of the narial flap when crossed with narrow nostril fails to activate in fully half of the offspring. Finally, cases are not unknown, as in certain rumpless fowl, when the dominant inhibitor has failed to act in the heterozygote completely. Several such cases have in recent years come to light and it has been said that they show a *reversal* of dominance, *i. e.,* the normally recessive character has become dominant. Such an expression runs counter to the modern interpretation of dominance, which is that dominance depends on the presence of a determiner, recessiveness on its absence. Clearly a given character can hardly be now due to a determiner and again to its absence. The more reasonable hypothesis is that a determiner, though present, may fail to complete its ontogeny.

An insight into the cause of this failure is given by modern studies in cytology and breeding. These indicate that, ordinarily, in pure races, a well-developed, purebred character has a double determiner as its embryological anlage, while in the heterozygote the determiner is simplex. Now in just these cases when the anlage is simplex the character develops imperfectly; and it is not difficult to understand how, under certain circumstances, the simplex determiner might be insufficient for the development of the organ. Such would result in complete failure to dominate, not a reversal of dominance.

Further proof that dominance is not reversed, but only weakened, is derived from the facts of retardation in the ontogeny of some heterozygotes. For example, the white of the Leghorn is dominant over black, but, in the females at least, the dominance is so imperfect that the plumage of the hybrid shows many black spots or is spangled or it may be of a uniform blue; but in later molts it becomes pure or nearly pure white. Similarly, Lang found that the hybrid snails between the red and yellow forms sometimes showed at first the recessive yellow, but later gained the dominant red. The ontogeny of the heterozygote characteristic thus appears retarded and frequently fails altogether to reach its final goal.

This failure of the simplex determiner of the heterozygote to develop the corresponding characteristic is frequently found in one sex and not in the other. For example, the simplex determiner for horn production in sheep suffices to induce horns in the males but not in the females. In the same way the simplex determiner induces color blindness in males but nothing less than the duplex determiner suffices to stimulate color blindness in females. One may say that, under the influence of testicular internal secretions the simplex determiner suffices for development, but not otherwise. No doubt the same is true for many other cases of "sex-limited heredity."

Imperfection of dominance goes even further. It is evinced not only in the heterozygote but even in pure-bred stock. This is the same as saying that, in breeding pure stock, a character may fail to develop even when a double determiner is present. Thus, in pure bred strains of Houdans or Dorkings having 5 toes on each foot, from 3 to 4 per cent. of the offspring fail to develop the extra toe on either foot. In certain races, at least, such as my Tosa fowl, two parents, both with complete inhibition of foot feathering, may have offspring in which this inhibitor fails to activate, so that their feet are slightly feathered. These cases of failure of a duplex determiner to work itself out in ontogeny are of the nature of sports—at least many sports are of the nature of defects arising in a pure-bred strain. In poultry one frequently gets such defects as failure of the neural tube to close (spina bifida), failure of the lower jaw to develop, absence of appendages and so on. In man, imbecility seems sometimes to occur as a sport; and it is doubtless a typical defect, transmitted as a recessive quality. It is probable that the same is true of hairlessness in mammals and man (Waldeyer, 1884, page 114, and Davenport, *Science*, November 20, 1908, p. 729). Since characteristics may occasionally fail of development in homozygotes their regular imperfection in heterozygotes is easier to understand.

Important consequences flow from the complete failure of a heterozygous characteristic. The first is, as pointed out by Shull, the difficulty of determining in the first hybrid generation what is recessive—since impotent dominance and recessiveness yield the same result. Indeed, one might be tempted to conclude with Shull that when a character regularly fails to dominate it will never be practicable to distinguish the dominant and recessive conditions. But the situation is not so desperate as that —one clear difference between dominance and recessiveness remains, namely, while the dominant character, even when of duplex origin, sometimes develops fully, sometimes imperfectly, sometimes fails altogether; the homozygous recessive condition yields, on the other hand, offspring with entire absence of the quality. Since we can not know our homozygous recessives in advance the practical method of determining them is as follows: mate similars; some will yield families that show a great range of variation in the given characteristic from high development to complete absence, such are dominants or heterozygotes; others will yield families that show a limited range of conditions and will all be like the parents—such are homozygous recessives. Their progeny are uniform because absence of a character can not show a variability in ontogeny.

The foregoing principle may be illustrated by an example. In polydactyl strains no family (of over 2 individuals) from two syndactyl parents fails to produce some normal children, but several families from two non-syndactyl parents produce in a total of 119 offspring no syndactyl individual. The invariable families are certainly the product of two recessive parents.

The fact of imperfect dominance bears upon the controversy of alternative *versus* blending inheritance. When a booted fowl is mated to a clean-shanked one the offspring show grades of boot ranging from 0 to 9;—10 being the heaviest grade recognized. For example, when a Cochin is crossed with a White Leghorn the average grade of booting is about 4 on a scale of ten. Booting would seem to be a typical blending character. Yet the evidence of segregation is excellent. For, two extracted recessives (full-booted) beget no clean shanked offspring. $DR \times RR$ gives 50 per cent. of the offspring of grade 5 or over, $DR \times DR$ yields 25 per cent. of grade 5 or over, while $DR \times DD$ gives none in these grades. A similar result is found in the apparently blending character of nostril height. May not segregation occur in the cases of apparent blending? Does not true blending occur only in complex characters such as stature and skeletal weight? Of such character complexes the component units may still segregate.

Finally, the fact of imperfect dominance leads to an explanation of many puzzling cases of apparent failure of inheritance. Some years ago I bought two tailless cocks *A* and *B*, of which *B* was said to be the son of *A*. They were certainly very similar in appearance. I mated *A* to some tailed hens and their offspring were tailed. The next year I mated these hybrids with each other and the females with their father. Were taillessness recessive, as I suspected, one-fourth of the progeny of the first mating and half of the progeny of the second should have been tailless. Actually there was produced not one tailless bird. One would apparently have been justified in concluding that taillessness is not an inheritable condition. But when the second tailless cock was mated with the tailless hybrids approximately half of the offspring were tailless; and such tailless offspring bred *inter se* have in turn produced a large proportion of tailless progeny. This whole case at first seemed inexplicable to me, as it did to Professor Bateson, to whom I related it, but it receives a satisfactory interpretation on the theory of imperfect dominance. For rumplessness, or rather an inhibitor of tail growth, is dominant over its absence. But with cock *A* this inhibitor is so impotent that in the heterozygote, at least, it does not make itself felt and even in the second hybrid generation the duplex determiner fails to activate fully. I say *fully*, for there was a trace of activity. At least fifteen per cent. of the offspring were recorded as having a small uropygium and in many of the adults the back appeared shortened and bent and the tail drooped instead of standing erect. Despite these evidences of the activity of the inhibitor, the striking fact is that its activity is so feeble that it cannot prevent the development of the tail. In the case of the second cock, however, the inhibitor is stronger and behaves more nearly according to Mendelian expectation. Now, if a character can be so feeble as to fail completely in development in the heterozygote and even in the homozygote it will give the impression of non-inheritability; and I have little doubt that many cases in which there is apparently no or only a slight inheritance are due to a weak determiner. I could cite a considerable number of cases of this sort in my experience, but I refer for an account of them to a book that is being published for me by the Carnegie Institution of Washington. Still one other lesson may be drawn and that is the apparent variability in what I call the *potency* of determiners. The evidence for this potency seems to me to be strong, as it certainly is important for an interpretation of all non-Mendelian cases of heredity. By the aid of the facts of imperfection in dominance and the hypothesis of varying potency of determiners the territory to which the principle of the segregation of determiners is applicable becomes greatly extended.

EXPERIMENTAL EVIDENCE ON THE EFFECTIVENESS OF SELECTION[1]

PROFESSOR H. S. JENNINGS

JOHNS HOPKINS UNIVERSITY

IN studying the problems of evolution in the common infusorian *Paramecium,* I found that by methodical and progressive selection striking results can be reached.

From a wild culture it is possible by progressively selecting in two opposite directions to obtain finally two lots, one of which is many times as large as the other, and the differences between the two are permanent and hereditary. By properly regulated selection a great variety of permanently differentiated lots are obtainable.

Throughout this work Galton's law of regression was found to hold; that is, the progeny of extreme parents inherited the peculiarities of their parents, but in a less marked degree. Furthermore, the results were such as to lend themselves readily to interpretation as exemplifying Galton's law of ancestral heredity.

Thus the effectiveness of selection was clearly demonstrated. But just what sort of effectiveness does the theory that selection is the dynamic factor in evolution demand? It demands that selection shall so act that it might finally produce progress from *Amœba* up to man. It must produce, from a given condition, something that did not before exist in that given condition.

Has selection so acted in this case? To answer this question, we must evidently know precisely what exists in the condition with which we start. We therefore next work with the progeny of a single individual—forming a "pure line," the characteristics of which we thoroughly know.

Now we try the effects of selection on this pure line.

---

[1] A paper read before the American Society of Naturalists, December 29, 1909.

Not the faintest trace of effect is produced, even by long-continued methodical selection for hundreds of generations. The race or line is absolutely permanent, so far as the appearance of any hereditary differences are concerned. The individuals of the line do indeed differ greatly among themselves, but these differences are not inherited; they furnish absolutely no foothold for selection.

Examination showed that *Paramecium* consists of many such races, differing among themselves slightly, but each race as unyielding as iron. And the extreme races found in the wild culture are precisely the extremes obtainable by long-continued selection.

The effects of selection have then consisted simply and solely in isolating races that already existed. It had produced nothing new; there had been no progress that would form a step, however slight, in the journey from *Amœba* to man.

When I had reached this point I looked about and found that others had been having similar experiences. The investigator who discovers these things for himself finds perhaps that

> Es ist eine alte Geschichte
> Doch bleibt sie immer neu.

And the second line is as true as the first, for to one who has put months and years on such attempts to accomplish results by methodical selection, its utter powerlessness comes with new and surprising force. Johannsen in working with beans and barley, Hanel with *Hydra,* had found many pure lines existing in nature, but as in my own case, each pure line was absolutely unyielding.

But we know that others *had* found selection effective; a whole series of cases comes at once to our lips. Galton in studying peas and men; Fritz Müller with maize; de Vries with maize and with buttercups, MacCurdy and Castle with guinea pigs and rats—all these had reported definite progress as a result of methodical selection.

Why this difference? Is there one law for the Jews, another for the Gentiles?

Looking into the matter with care, we find that the results with our own material are, after all, like those of the investigators mentioned if we treat it in the same way. None of these workers first isolated their pure races. If we begin with a mixture we can, in beans, in barley, in *Paramecium,* in *Hydra,* by a methodical process of slow selection make gradual progress in a certain direction. But our selection is only a process of purification, and when we finally get a pure race, selection is utterly powerless to go farther. We should have been completely in the dark as to the real effect of selection if we had not carried through rigidly the "pure line" idea.

Is it possible then that we have in this pure line idea an instrument of the greatest importance for analysis? Is it perhaps the key which every one must have in order to understand the results of selection? May it be indeed one of those fundamental ideas which, like the idea of mutation, is fitted to clear and crystallize a confused and turbid mixture? Is it possibly of sufficient importance to deserve agitating a little before the American Society of Naturalists?

Let us put these questions to the practical test; let us apply the idea as an instrument for the dissection of the classic cases which seem to demonstrate the efficacy of selection in producing change of type.

Johannsen in his recent book has used the pure line concept as an instrument for analysis of the entire field of variation, heredity and evolution, and to him is due the credit of first perceiving the importance of this concept, when sharply defined, as such an instrument for research and presentation. The work of Johannsen, I believe, will remain one of the landmarks of progress in this field. But my own analysis has been independent of Johannsen's and diverse from it, developing inevitably from what I have myself seen, so that I may venture still to present some of its results.

But how can we apply the pure line idea to organisms whose lines are *not* pure; organisms that interbreed freely; organisms in which the characters of a given line split off, separate, and become exchanged for those of other lines, in the way characteristic of Mendelian inheritance?

The pure line idea here becomes a little elusive, a little abstract. But possibly it is still helpful as an instrument of analysis; let us try it. In order not to emphasize purity where impurity is the rule, let us substitute Johannsen's term *genotype* for "pure line"—defining the genotype as a set of individuals which, so long as they are interbred, produce progeny that are characteristically uniform in their hereditary features, not systematically splitting into diverse groups.

Now, how can we determine whether the genotype concept, with its consequences for the effects of selection, applies to organisms with biparental inheritance? Reflection shows that if it does, certain general propositions are true: if these propositions are found to hold, the genotypic explanation of the effects of selection is confirmed.

1. The first proposition is this: Organisms in which selection has shown itself effective are composed of many genotypes; of many races that are diverse in their hereditary characters. This we know to be true.

2. Second, from such a mixture of genotypes it is possible to isolate by selection any of the things that are present—perhaps in a great number of different combinations.

3. But from such a mixture it is *not* possible to get by methodical selection anything not present (save when rare mutations have occurred).

4. Therefore it is not possible to get by methodical selection anything lying outside the extremes of the genotypic characters already existing.

This is perhaps practically our most important proposition. For in order that selection shall produce progression from *Amœba* to man, it is evidently necessary that it should give us characters lying beyond the extremes of what already exists.

5. Our fifth proposition is that in the case of genotypes that cross-breed readily, we may get an indefinite number of combinations of all that lies between the extremes of the existing genotypes—the variety of combinations realized depending on the rules of inheritance.

Now, if we test by these propositions the classic cases of effective selection, what is the result?

Galton's work with peas and with men yields at once to the analysis, giving precisely the results which the genotypic idea requires. A by-product of the analysis is the practical evaporation of the laws of regression and of ancestral inheritance so far as their supposed physiological significance is concerned;[2] they are found to be the product mainly of a lack of distinction between two absolutely diverse things—between non-heritable fluctuations on the one hand, and permanent genotypic differentiations on the other.

The experiments of Müller and de Vries on maize yield with equal readiness. In these cases the male parents are unknown; the freest sort of crossing was occurring, and what selection did was pick out the progeny of extreme male genotypes, till the result approached the limit of the most extreme existing genotype under the cultural conditions.

MacCurdy and Castle's experiments in changing by selection the color-patterns of rats and guinea-pigs dealt with races of complicated descent; they plunge us at once into all the difficulties due to interweaving, blending and transfer of characters from one genotype to another. But if we stick closely to the general propositions already stated, we shall have a guide. MacCurdy and Castle got by selection all sorts of conditions lying between the extremes with which they started. But did they get anything lying outside these extremes, as would be required in order to show that we can by selection make evolutionary progress? As I read their results, they did *not*. Their experiments are most important for many problems of variation and inheritance, but they do not give us evidence that methodical selection can produce anything beyond combinations of what already exists; hence they do not help us in getting from *Amœba* to man.

---

[2] This significance was supposed to lie in showing that the characteristics of the progeny depend upon the characteristics of the ancestors for many generations back, in ways that are definable. "Mr. Galton's view of the effect of regression follows inevitably from the general theory of chance, if we regard the character of an individual as a phenomenon due to a series of complex groups of causes, *among which are the characters of each ancestor.*" (W. F. R. Weldon, *Biometrika*, I, p. 370.)

The law of ancestral inheritance does not hold in pure lines, even in a statistical sense, as has repeatedly been shown. The progress of a long series of extreme ancestors does not differ from those of a series of average ancestors.

The work of the German breeders who have for years practised methodical selection for improvement of agricultural races clears up at once under the genotype idea, as the analyses of Fruwirth, v. Rümker and others show us. Continued methodical selection is often necessary, but what it does is to purify a contaminated race—a process which, owing to the laws of inheritance, may require several generations.

I have spoken only of those experiments which seem at first view to show the efficacy of selection; brevity requires me to pass without mention over investigations which, while not carried on with pure lines, support and reinforce the conclusions drawn from such work. Such for example are the fundamental experiments of Tower, the recent work of Pearl, of Shull, and many of the experiments of de Vries.

Thus far the dissecting knife of the pure line idea succeeds admirably in letting the light into the obscure workings of selection. Any one who uses it with precision will find what an important advance its exact formulation by Johannsen marks over even such an analysis as that given by de Vries. In the work of de Vries, as in that of many recent authors, the selection idea is appraised at essentially its true value, but much in its action is left obscure. The reader is surprised at the accounts of experiments in which selection does accomplish marked results, though according to the general theory, it should not; one is left puzzled in judgment as to what we may expect from it. With the sharply formulated pure line concept as a guide, most of this obscurity disappears.

And then, to keep us from resting on our oars; to give us humility and spur us to further work—we come to the one case in which the pure line idea fails to bring clearness. This is de Vries's experiment with buttercups. Here, after selection the extreme was moved far beyond that before selection. Before selection the extreme number of petals was eleven; after selection it was thirty-one. Before selection no single individual had an average number of petals above six; after selection the average of all was above nine, and some had an average of thirteen! It is true that there are "mitigating circumstances" here; the work was not done with pure lines, and the variations dealt with are not of the ordinary fluctuating sort (as de Vries points out); change in cultural conditions doubtless played also a large part. Possibly repetition with thorough analytical experimentation will show that something besides selection has brought about the great changes. But at present the case stands sharply against the generalizations from the pure line work. It is the only such case that I have found.

To sum up, one finds not only that his own results and those of many other modern workers give the pure line interpretation, but also that all other cases that had seemed to point the other way yield readily to the genotypic analysis—save one. If we ride rough shod over this case, as not yet sufficiently studied, then we may draw a tentative conclusion as follows:

The pure line or genotype idea is the one to see clearly and grasp firmly in experimental investigations on selection. Many even of the modern experiments remain obscure in their significance simply because the workers have not grasped this concept, have not shown the relation of their results to it. Further, in presenting one's own work, or in interpreting the accounts of others, the genotype concept is the instrument of precision to take in hand. The results of the analysis made by its aid indicate that most or all of the experiments in methodical selection have consisted in shifting about, isolating and recombining preexisting, permanent hereditary differentiations, giving results that were interpreted as revealing the law of actually progressive evolution, though in reality they had no relation to such a law.

To our conclusion as to the analytical value of the pure line idea we may expect strenuous opposition on the part of that last small remnant (if there be such a remnant) of the biometrical school that still submits to the dictation of Pearson[3]—for by one of those sardonic paradoxes through which nature revenges herself, the men who from outside have lectured biology on the necessity of becoming exact are the strongest opponents of exact experimental and biological analysis—seeming to feel that mathematical treatment renders other kinds of exactness undesirable.[4] Those who find the genotype idea useful may then prepare themselves for one of those justly famous bludgeonings from the dictator of the whilom orthodox biometrical school; this is the last honorable mark of distinction which stamps the investigator as a thorough and exact analyst of things biological.[5]

---

[3] Note how quickly the biometricians that devote themselves to careful biological investigations fall away from the Pearsonian faith. Darbishire, Davenport, Tower, Shull, Johannsen, Pearl; are there any biologists of achievement that still hold with Pearson?

[4] Pearson in 1901 informs us that evolution is a field "where no tabulation of individual instances can possibly lead to definite conclusions" (*Biometrika*, I, p. 344). This was the year of the appearance of de Vries's *Mutationstheorie*, and of the revival of Mendelism. Compare in definiteness and value the conclusions drawn from the work inaugurated in these two lines, based as it was precisely on the "tabulation of individual instances," with those from the biometrical work, with its careful avoidance of "individual instances."

[5] To name the men who have been subjected to Pearson's most savage

A word more on certain general questions. Can we conclude that if selection has no dynamic effect in changing existing genotypes, that therefore it need not be reckoned with in evolution? Or must we conclude that if it is to be reckoned with at all, selection has opportunity to act only on large leaps in evolution; that evolution takes place by such leaps, and not by imperceptibly small changes?

Such evidence as the pure line work gives implies neither of these things. The differences between the diverse pure lines *have* arisen in some way, if evolution occurs, and once these differences have arisen, they are open to the operation of selection as are any other differences. What the pure line work shows (agreeing in this with other lines of evidence) is that the changes on which selection may act are few and far between, instead of abundant; that they are found not oftener than in one individual in ten thousand, instead of being exhibited on comparing any two specimens; that a large share of the differences between individuals are not of significance for selection or evolution—these being precisely the differences measured as a rule by the biometrician's "coefficient of variation." Thus the work of natural selection is made infinitely more difficult and slow; but logically it is still possible.

Nor does the pure line work assist natural selection, as some have hoped from the mutation work, by making the steps in evolution greater in amount. On the contrary, the work with genotypes brings out as never before the minuteness of the hereditary differences that separate the various lines. These differences are the smallest that can possibly be detected by refined measurements taken in connection with statistical treatment. Johannsen found his genotypes of beans differing constantly merely by weights of two or three hundredths of a gram in the average weight of the seed. Genotypes

assaults is to name the men that have done most to advance our knowledge of heredity. The cases of Castle and of Bateson will occur to every zoologist.

of *Paramecium* I found to show constant hereditary differences of one two-hundredth of a millimeter in length. Hanel found the genotypes of *Hydra* to differ in the average number of tentacles merely by the fraction of a tentacle. That even smaller hereditary differences are not described is certainly due only to the impossibility of more accurate measurements; the observed differences go straight down to the limits set by the probable error of our measures. Genotypes so differing have not risen from one another by large mutations. The genotypic work lends no support to the idea that evolution occurs by large steps, for it reveals a continuous series of the minutest differences between great numbers of existing races.

All together, I think we may say that the pure line or genotype concept presents an instrument of analysis which is worthy, on the basis of what it has thus far done, of a thorough tryout for future work, and no one interested in these questions can afford to neglect it. This conclusion is quite independent of the concrete results reached; the efficacy of selection in modifying genotypes may be demonstrated to-morrow, but the demonstrators will need to show precisely the relation of their results to the pure line concept.

THE ARTIFICIAL PRODUCTION OF THE PARTHENOGENETIC AND SEXUAL PHASES OF THE LIFE CYCLE OF HYDATINA SENTA

A. FRANKLIN SHULL

COLUMBIA UNIVERSITY

THE causes that determine the transition from the parthenogenetic to the sexual mode of reproduction in the rotifer *Hydatina senta* have been the subject of a number of investigations, which have led to contradictory conclusions. Maupas was led to attribute the appearance of sexual forms to changes of temperature, Nussbaum to starvation. Punnett found that neither temperature changes nor starvation had any effect, but obtained what seemed to be distinct strains, each producing a fairly constant proportion of sexual forms, regardless of external conditions. One strain produced many sexual females (about 40 per cent.), another few sexual females (2 per cent.), and a third none at all. His conclusions regarding temperature and starvation were supported by Whitney, but the latter worker obtained no evidence of strains, finding that so-called strains of one type might break up into those of any other type within a single parthenogenetic series.

I believe I have evidence which may explain the difficulties hitherto encountered, evidence that goes far towards bringing the previous contradictory conclusions under a single point of view. I shall attempt to show in this brief presentation that the presence of substances in the water, other than food, exerts a strong influence on the inauguration of the sexual phase.

In this paper I shall speak of the male-producers as sexual females. The identity of the two has long been suspected from certain numerical relations, but more direct observations have been wanting. I have now, however, been able to secure winter eggs and males from the same parent. Since in all cases known, a female lays parthenogenetic eggs of only one sex, there can be little doubt that sexual eggs and male eggs are identical.

To test the influence of substances in the food cultures, lines of rotifers were reared in the water of some old cultures, from which the protozoa had been removed by filtering. Various dilutions of this water were used, one fourth, one half, three fourths and undiluted, as well as pure spring water. The same kind and quantity of food, a flagellate, *Polytoma uvella,* was added to each, and was found to live readily in all concentrations of the filtrate. The results of eight or more generations bred simultaneously under these conditions are shown in Table I.

TABLE I

	SPRING WATER.		OLD CULTURE FILTRATE.							
			One fourth.		One half.		Three fourths.		Undiluted.	
	Sex. ♀	Parth. ♀	Sex. ♀	Parth. ♀	Sex. ♀	Parth. ♀	Sex. ♀	Parth. ♀	Sex. ♀	Parth. ♀
	26	177	25	407	15	350	8	362	0	337
Per cent. Sex. ♀	12.8		5.7		4.1		2.1		0.0	

There is a gradual decrease in the proportion of sexual females from the line bred in pure spring water to that in the undiluted filtrate. The series in the dilute filtrate were discontinued at this point, but those in spring water and in concentrated filtrate were continued. In the latter line, nineteen complete generations were obtained without a single sexual female, while in spring water the sexual forms recurred at intervals, though not frequently, to the end of the experiment.

The experiment was repeated by removing to spring water a female of the seventh generation of the series bred, in the preceding experiment, in concentrated filtrate. The results of this change are shown in Table II. Six generations were reared in each line.

TABLE II

SPRING WATER.			OLD CULTURE FILTRATE.		
Sex. ♀.	Parth. ♀.	Per cent. Sex. ♀.	Sex. ♀.	Parth. ♀.	Per cent. Sex. ♀.
33	216	13.2	0	174	0.0

From the third generation of the series in spring water in Table II, a female was returned to the concentrated filtrate, and her progeny reared for three generations. A control was continued in spring water. The results are those in Table III.

TABLE III

SPRING WATER.			OLD CULTURE FILTRATE.		
Sex. ♀.	Parth. ♀.	Per cent. Sex. ♀.	Sex. ♀.	Parth. ♀.	Per cent. Sex. ♀.
7	110	5.9	0	107	0.0

The experiment was repeated four times, with sisters in each case, derived from lines more or less distantly related to those in the preceding experiments. These are recorded in Table IV.

TABLE IV

No. of Exp.	SPRING WATER.			OLD CULTURE FILTRATE.		
	Sex. ♀.	Parth. ♀.	Per cent. Sex. ♀.	Sex. ♀.	Parth. ♀.	Per cent. Sex. ♀.
1	44	163	21.2	0	141	0.0
2	49	64	43.3	0	128	0.0
3	7	106	6.1	0	103	0.0
4	5	76	6.1	0	85	0.0

In every case, the evidence points to the same conclusion, namely, that the filtrate from the old cultures reduces the number of sexual females. The losses by death are too few to account for the results obtained, and there is evidence to show that what deaths there are are not selective.

It is interesting to note the bearing of the above evidence on the question of starvation. It is not practicable to diminish the quantity of food placed in the dishes, without at the same time diminishing the quantity of other substances introduced. Several experiments were made to test the apparent effect of starvation. When the young were isolated, they were given only as much food as was judged necessary to support life and enable them to produce a moderate family. A control line, which was fed abundantly from the same cultures, was maintained in each case. One experiment, Table V, included 55 generations and covered a period of three months. In this time, the well-fed control varied so greatly in the proportion of sexual to parthenogenetic females produced, that it is important, not merely to note the totals, but to divide the experiment into periods, and compare the results in each.

TABLE V

Limiting Dates.	WELL-FED.			STARVED.		
	Sex. ♀	Parth. ♀	Per cent. Sex. ♀	Sex. ♀	Parth. ♀	Per cent. Sex. ♀
July 23–July 27	127	73	63.5	72	47	60.5
July 28–Aug. 25	50	754	0.6	125	265	32.0
Aug. 26–Sept. 5	129	153	45.7	55	80	40.7
Sept. 6–Sept. 20	35	203	14.7	34	100	25.3
Sept. 21–Oct. 12	187	261	41.7	93	157	35.2
Oct. 13–Oct. 25	25	208	10.7	87	161	35.0
Total	553	1,652	25.0	466	810	36.5

While the experiment as a whole shows a decidedly higher percentage of sexual forms in the starved families, there are parts of it that show a slightly lower proportion in the starved line. The variation in the percentage of sexual females from one period to the next in the starved line is of the same sign as in the corresponding periods of the well-fed line, but is smaller in every case. While the major fluctuations of the starved line occur simultaneously with those of the well-fed line, they are less in degree; the extremes of the starved series are always well within those of the well-fed. I can find only one factor which operated on both lines in the same way, but to less degree in one line than the other, namely, the food culture.

Of especial interest are the second and sixth periods Table V. In these, not only the *percentage*, but also the *absolute number*, of sexual females is higher among the starved individuals. This shows that the percentage is not raised by the mere elimination of some of the parthenogenetic females.

The experiment with starvation was repeated three times, each repetition including eight to sixteen generations. Each time there was a considerably higher proportion of sexual females in the starved families.

While it is conceivable that several factors may be at work producing these different proportions of sexual to parthenogenetic forms in the well-fed and starved families, the experiments with the filtrate from old food cultures show that the different quantity of dissolved substances incidentally given with the food is sufficient to explain the results. If this is the correct interpretation, the larger proportion of sexual forms in the starved families is not due to lack of food, but to the absence of chemicals which, in the well-fed families, prevent the appearance of the sexual forms.

THE SIGNIFICANCE OF THE COURTSHIP AND SECONDARY SEXUAL CHARACTERS OF ARANEADS[1]

PROFESSOR THOS. H. MONTGOMERY, JR.

UNIVERSITY OF PENNSYLVANIA

But few observers have made special studies in those phenomena in spiders of which it is proposed to treat in the present communication. The first studies, by Canestrini, were inaccessible to me. The main work on the subject is that of Professor and Mrs. Peckham (1889, 1890). They have described in great detail the courtship of a considerable number of Attidæ, and have given excellent illustrations of the attitudes of the males. Then after an analysis of the phenomena in question they have criticized the views of Wallace (1889), and have accepted that part of the sexual selection theory of Darwin which accounts for secondary sexual differences on the basis of an esthetic discrimination by the female. The results of these studies have been generally accepted as one of the strongest confirmations of Darwin's views. In the introduction to their last memoir (1909) they have reiterated their arguments, with the addition of certain new and important observations. The next special work on this subject is my paper of 1903, in which is described in detail the courtship of certain lycosids, agelenids, dictynids, theridiids, pholcids, epeirids and thomisids. My general theoretical conclusions were quite different from those of the Peckhams: the adult male is excited simultaneously by fear of and desire for the female, and his courtship motions "are for the most part exaggerations of ordinary motions of fear and timidity. By such motions he advertises himself to the female as a male, but there is no proof that he consciously seeks to arouse her eagerness by esthetic display . . . there seems to be no good reason to hold that the female is actuated in her choice by sensations of beauty.'' Thus my opinion was opposed to Darwin's theory. The remainder of the literature on the secondary sexual phenomena of araneads contains for the most part only casual observations, without attempts at analysis.

---

[1] This paper was presented before the American Society of Naturalists, Boston, Mass., December 29, 1909.

I. Some General Mating Relations

For a correct understanding of the points at issue it would be very desirable to have ample data on the numerical proportions of the sexes, but unfortunately little is known on this head. What is known is brought together in another paper of mine (1908*a*); and there also it was found in the case of *Lathrodectus mactans* that the ''average male ratio (number of the males divided by the number of the females) is 8.19, determined from a count of 41,749 newly hatched spiderlings.'' In this species the adults differ most markedly, and the young emerging from a cocoon are readily separable into two groups, distinguishable not only by size relations, but also, as specially indicated by me, by differences in the form proportions of the abdomina. Those spiderlings with a flatter dorsum and more anterior pedicel were considered to be males, for this is one of the characters in which the adults differ. However, none of these spiderlings were raised to maturity, though the attempt was made to do so; no differences in the internal genital organs can be found at the time of hatching, and occasionally (though rarely) nearly intermediate forms occur between the two groups of spiderlings. There is then room for doubt whether the two groups represent males and females, respectively, and the sex-ratio is not securely established from my results; it is rather in the nature of a strong probability. Beyond this case nothing definite is known about the numerical proportions of the sexes.

It is the general rule that the males mature earlier than the females, and the former do not live longer than a year. Promiscuous mating is general, a male impregnating a number of females, and a female receiving a number of males. I have seen a female of *Geotrecha pinnata* mating with two males in close alternation, two males of the theridiid *Ceratinopsis interpres* embracing a female simultaneously, and I have described (1903) for *Theridium tepidariorum* as many as twenty-seven impregnations of one female. In the attid *Phidippus purpuratus* one male was seen by me to fertilize several females. Monogamy is exceptional, and would appear to occur in cases where the male seizes immature females by force, and where the male lives in a mating nest with a female. Many attids make such nests; in the case of *Phidippus purpuratus* I have frequently found pairs in such nests in the wild state but never found them to make such nests in captivity, where there is on the contrary promiscuous mating. McCook (1890) has brought together some of the literature on mating nests. In certain cases an adult male seeks out and sequestrates an immature female, mating with her when she matures. The Peckhams (1889) found the only attid under their observation, "in which we saw males take possession of young females and keep guard over them until they became mature," to be *Philæus militaris*. A pair of *Drassus neglectus* was caught by me in a mating nest on June 16, last, and placed in a cage, where he built another nest around her; on June 23 he mated with her when she had just finished moulting and was still quite soft; in another case a male and an immature female were found in the same nest. A mature male of another drassid, *Prosthesima atra,* was repeatedly observed by me to hold an immature female, and on another occasion to grasp two such at once. In *Theridium tepidariorum* adult males wait upon the snares of immature females, and this has been seen by McCook (1890) and me in various epeirids. In *Lycosa ocreata* I found that males pay no attention to immature females, while they do in *L. scutulata.* During the past summer I have seen males courting immature females in the attid *Zygoballus beltini,* the thomisid *Xysticus nervosus,* and the drassid *Chiracanthium inclusum.*

In some species, as notably epeirids and lycosids, pregnant females are hostile to males. But I have seen such females of *Theridium tepidariorum* and *Phidippus purpuratus* receive males, and on one occasion a female of *Geotrecha pinnata* was interrupted several times during her cocooning by embraces of a male. Males appear to court any mature female, whether she be virgin or not.

II. SENSES EMPLOYED IN SEXUAL RECOGNITION AND STIMULATION

Here we have to consider briefly the rôles of hearing, touch, sight and smell.

There is no good evidence that spiders possess hearing, while the arguments of Wagner (1888) and especially the direct observations of Pritchett (1905, done under my direction) speak almost conclusively against such possession. Some spiders have stridulating organs, and in certain species these are limited to the male (*Theridium,* according to Westring), but no experiments have been made to determine whether the spiders react to the sounds produced thereby. I have recently found in the drassid genus *Geotrecha,* where both sexes possess a stridulating apparatus, the spiders do not in any way indicate any perception of sound but perceive each other solely by touch. It is then fairly firmly established that the sexes do not recognize each other by hearing.

Touch is the dominant sense, and would appear to be the especial function of the jointed spines. In nocturnal species as well as in all snare-weavers it appears to be the only sense of sex-recognition.

Smell is possessed by spiders, but what organs subserve it is not determined, beyond that it seems to be distributed over a considerable area of the body. The most careful study of it has been made by Pritchett (1905), while Petrunkevitch (1907) found it to be less keen than touch. It might be this sense that guides wandering males in their search for females. But I am inclined to believe it does not, for of pairs I have watched attentively in cages the male always appeared to find the female by either touch or sight, while if he is near her, but without seeing or touching her, he seems unconscious of her proximity. Further, when in the wild state a male approaches a female upon her snare, there seems to be no evidence that he constantly approaches her in the direction of the wind. Thus it is very doubtful whether scent has any part in sex-recognition in spiders, while it is the most usual mode of sex-recognition in insects.

Sight undoubtedly plays a considerable part in sex-recognition in certain diurnal species, determined for the attids by the Peckhams, and for the lycosids by me. These spiders, however, perceive readily only moving objects. But, as we shall see, it is not used for this purpose in the other spider families, not even in the diurnal thomisids. Thus I can not agree with Petrunkevitch's conclusion (1907) that "the sense of sight is beyond any doubt the only sense that guides hunting spiders on their hunting excursions and in finding the females during the mating period," for I have frequently noticed males of even diurnal attids and lycosids first recognizing the female by touch. And in the case of *Pardosa nigripalpis*, a species that always courts by light, it was remarked by me (1903): "In a double cage with a transparent glass partition, a male in one compartment and a female in the other, I have not seen a male court a female, though he certainly sees her through the partition; probably, then, it is touch of a female that impels him to courting activity." Numerous pairs were kept by me in such cages to test this point.

The senses of sex-recognition are, accordingly, touch in the first place and sight in the second, the latter important in only a few families.

III. Details of the Courtship Phenomena

It will be convenient for our present purposes, for it is based upon habitudinal differences, to divide the species on which observations have been made into the two categories of "snarers" and "hunters." The literature on the subject has been gleaned as thoroughly as possible; and my new observations of the past summer have been presented more fully than the others simply because they are here given for the first time.

1. *Snarers*

In *Dictyna volupis* Keys. mature males and females live together upon the web, which they appear to fabricate in common; the male is somewhat larger. In two cases the approach of the sexes was seen by me (1903): in one the male approached and seized the female; in the other case a male came face to face with a female, "then, each of them tapping upon the web with the first two pairs of legs, they moved backward and forward slowly. This lasted only two minutes, when they both became quiet half an inch apart; it was repeated again for a short period." These are the only observations on any cribellate form, and they do not indicate clearly whether rape or courtship by the male is the usual process.

For the Agelenids Menge (1843) described the approach of the male in *Agelena labyrinthica* as follows: The male climbs into the web of the female, taps on it with his palpi, but must sometimes wait for an hour before the female allows him to approach. "When she is complacent she places her legs close to her side, and the male embraces her with his legs and carries her into the funnel." In *A. nævia* Walck., I saw the approach of the male in two cases; in both there was nothing "to indicate a courtship; there was simply a cautious approach of the male," he touched her with his first legs, "and after he had found no sign of hostility on the part of the female he quickly seized her, and she was absolutely submissive in his grasp." In *Tegenaria durhami* Scop., in several cases, the male was seen by me to slowly approach the female upon her web, he tapping the latter with his fore legs as he advanced, the female occasionally also tapping in response, after which he would make a sudden rush at her. In these agelenids there are no courtship motions beyond tapping on the web, to which the female may respond, in like manner; the male seems to find her by touch, and after a cautious approach to seize her forcibly.

In *Pholcus phalangioides* Fuessl. I found (1903) no courtship; the male approaches the female very cautiously upon her web, and touches her gently with his legs; he always approaches her from beneath, and immediately drops from the web if she move at his touch. He finds her position by carefully pulling the lines of the snare.

In the theridiids a number of observations have been described. Menge (1843) found in *Linyphia triangularis* that the approaching male shakes the snare rapidly, to which the female responds by a similar motion. In *Theridium tepidariorum* C. Koch I have seen (1903) the approach of the sexes many times; when a male is placed upon a web of the female, she immediately signals to him by repeated jerks upon the lines of the web, sometimes moving towards him. This signalling is a sign of eagerness on her part, and "she makes it at no other time than when she is eager and notices the approach of a male of her own species. . . . The whole attitude of the male is that of combined timidity and great eagerness. . . . He tests the eagerness of the female, and finds her position upon the web, by grasping with the claws of his first pair of feet the web lines that she is shaking by her signalling, and by drawing these web lines taut he feels her movements all the more distinctly; he approaches gradually nearer her, guided by her signalling, and finally makes a short rush toward her.'' The female often seems insatiable, even leaving food at times to approach the male, and the courtship is largely on her part, by signalling.

Similar signalling by the female was noticed by me in *Teutana triangulosa* Wolck. During the past summer I watched the process in *Theridium frondeum* Htz., where the female signals, and the male responds in the same way; the female had her rear turned towards him so that she could not possibly see him; in one case a female signalled to another female. In the case of the tiny *Ceratinopsis interpres* Emert. I placed two males and a female together in a vial, where they spun a maze of lines in a short time, but I observed quite a different approach of the males. The female does not appear to signal, but the male makes a quick rush at her, and taps her rapidly with his legs until she becomes submissive with contracted legs. A male acts towards her as he would to another male, seemingly aggressive, until she becomes immobile; they find one another by touch communicated along the web lines, not by sight.

In the Epeirids a number of genera have been studied. In *Pachygnatha listeri* Menge (1866) saw the male seize with his chelicera those of the female. In *Argiope* (Peckham 1889, McCook 1890, Emerton 1883) the male courts the female by pulling the radii of her snare, and she responds in the same way. ''If matters be favorable, the male draws nearer, usually by short approaches, renewing the signals at the bolting places. Sometimes this preliminary stay is brief; sometimes it is greatly prolonged'' (McCook). In the case of *Acrosoma gracile* Walck. I dropped (1903) a male upon the web of a female, and as soon as he touched her (within five minutes) he copulated; no special courtship was seen. In the genus *Epeira* the approaches of the male are well known from the observations of Walckenaer (1837), Menge (1843, 1866), Termeyer (1866), Lendl (1886), McCook (1890) and myself (1903, 1908*b*). The male approaches the female cautiously upon her web, locating her and testing her eagerness by pulls upon a radius, she responding gently to his signals when she is eager, otherwise she makes a sudden rush at him in which case he swings free from her web on a particular line of his own.

When we sum up what is known of snare-weavers, it appears that in them sex-recognition is always by touch, by tapping or pulling of the web. In a few cases (*Tegenaria*, *Ceratinopsis* and perhaps *Dictyna*) the male attempts to capture the female by storm; but more generally he approaches very cautiously and timidly, signalling to the female. When there is a courtship it is one of line signals, and sometimes (*Theridium*) the female seems the more eager and active in the courtship.

2. *Hunters*

For the drassids, most of which are nest makers and essentially nocturnal, there are the following observations. Menge (1872) placed together a male and female of *Melanophora nocturna*, whereupon the male immediately embraced the female without courtship; and he observed (1873) a similar forcible rape in *Chiracanthium oncognathum*. In *Clubiana trivialis* he found (1873) that the male makes a small saccular nest next that of the female, and that he knocks, sometimes for days, upon her nest wall before she allows him to enter. During the past summer the following observations were made by me. In *Drassus neglectus* (Keys.) an adult male appropriates an immature female, seals her in a mating nest, and mates with her just after her last moult; in one case the male found the female in the cage by touch alone (I could see no evidence of recognition by sight), and rendered her passive by gentle tapping with his first legs. The male of *Chiracanthium inclusum* Htz. also finds the female by touch, and tries to subjugate her by gentle tapping with his exceedingly long first leg pair. In *Prosthesima atra* (Htz.) the male appropriates immature females; there is no courtship, beyond a tapping with the legs. The two sexes of *Geotrecha crocata* (Keys.) do not recognize each other by sight; a mating was observed, but no courtship preceded it. Also individuals of *Geotrecha pinnata* Emert, do not recognize one another by sight, perceiving each other only when nearly in contact—so probably by air pressure (touch); they run rapidly, and in the open on overcast afternoons, so they might be expected to form visual images, but they showed no signs of recognizing each other by sight. After a mating the male always leaves the female for a few moments, then returns to her again, and at such times he moves in an irregular path, feeling for her. He recognizes her by contact, and taps her legs with his own until she becomes quiet. In one case a female accepted in succession and repeatedly the embraces of two different males, one of which had only a single palpus; here the female exhibited no choice whatsoever. In the drassids, accordingly, sex recognition is wholly by touch; the male sometimes seizes the female by storm, sometimes subjugates her by tapping with his legs.

In the thomisids we have to do with diurnal spiders that lie in wait for their prey, without constructing web lines (except drop lines); they are mostly found upon vegetation above the ground. The male is more nimble than the female and smaller, sometimes much smaller. In *Micrommata virescens* Menge (1874) saw the male jump upon the back of the female. In *Xysticus stomachosus* Keys. I found (1903) that the sexes recognize each other by sight to some extent, but that the male pays no particular attention to the female until he touches her, when he quickly seizes one of her fore feet with one of his and nimbly swings around and mounts her from the rear. Last summer I saw somewhat similar behavior in *X. nervosus* Banks: the male seemed to recognize the female only by touch, when he came in contact with her he immediately placed several of his feet upon her, she drew her legs close to her side and he got upon her dorsum. Also in *Misumena aleatoria* I saw, on several occasions, that the minute male always found the female by touch, and quickly climbed upon her. In this family, accordingly, even though diurnal, there is no courtship and the male gains the female by superior agility aided by his smaller size.

The lycosids comprise crepuscular and nocturnal species, few of them hunting in the sunlight. Menge (1877) observed a female of *Trochosa terricola* Thor. build a nest in moss, and a male lying for hours before this hole "striking lightly here and there with the palps and fore legs," after which the female allowed him to embrace her. A similar courtship was seen by Mrs. Treat (1879) in another lycosid, the species not positively identified; the female lives in a silken burrow which the male approaches very cautiously; she "slowly advances to meet him, and he slowly retreats from the mouth of the den, moving backward while she moves forward, just reaching him with the tips of her fore legs as if caressing him"; this backward and forward progression of the two is repeated many times. Observations on other lycosids have been made by me (1903). In *Lycosa bilineata* (Em.) (*L. ocreata pulchra* Montg.) the anterior male tibiæ are provided with thick brushes of vertical hairs, making them very conspicuous, but though the sexes recognize each other by sight there is no courtship; in one case a male simply jumped upon the female, in another after touching the female the male withdrew a little and quivered these legs slightly, the female moved towards him and he jumped upon her.

When the male stands before the female with these legs flexed, as he does, with the patellæ close to the sides of his cephalothorax and his body crouched near the ground, the tibiæ are more horizontal than inclined upward. This, then, is not the best attitude to exhibit them to the female. . . . On this account this bristling of the tibiæ can hardly be regarded as a sexual ornament that is exhibited to charm the female. Further, it may be noted that this position of the first pair of legs is also assumed by the female when roughly handled or frightened; it is an attitude of defense of the species, not of sexual exhibition.

In *Lycosa ocreata* Hentz (*L. stonei* Montg.) the tibiæ of the first legs of the male are similarly provided with a brush of hairs, and he is darker than the female, but there is a pronounced courtship by the male consisting of rhythmically repeated waving of these legs with a jerking of the whole body backward and forward. Sight plays a considerable part in the approach of the sexes, but "apparently the first recognition of sex is by touch" for the courtship does not commence until the male has touched the female. In *L. lepida* (Keys.) the male is smaller and more brightly colored, and exhibits a simple courtship, shaking in the air his fore-legs that are only slightly elevated above the ground (his body may be prone). In *L. scutulata* Hentz there is "a decided courtship; the male differs from the female in his smaller size and in the black color of a portion of his fore-legs, and these legs (and the palpi also) are moved in a particular manner during the courtship. Observation shows that the male recognizes the female as such at a distance of at least six inches. The male's approach to the female is very slow, a kind of creeping, not at all similar to the vehement approach of certain other Lycosids. . . . The female, if eager, gives the signal of willingness to the male by touching him lightly with her first pair of legs, when he immediately embraces. In the observed cases, with one exception, the female killed the male at the end of the copulation." In *Pardosa nigropalpis* Emerton the males are smaller, and there "is a marked sexual color difference, the male being deep black and the female more brownish. . . . The advances are made by the male, and there is a distinct courtship process, which a vigorous male may maintain for two or three hours at a time with few interruptions when the female is recalcitrant. . . . The courtship motions are as follows:

The male stands with his body well elevated above the ground (an attitude that the female takes only when she is aggressive) on his three posterior pairs of legs, his head higher than his abdomen. . . . He waves his palpi upward in the air (*i. e.*, straightening them out before his head) and flexes them outward, from one to three times, then draws his body slightly backward and downward, rapidly waving in the air the outstretched palpi and first pair of legs, and spasmodically shaking the whole body with the violence of the movement. . . . The male recognizes a female as such immediately on touch; whether he recognizes her by sight alone I can not tell. In courting a fleeing female the male appears to follow her mainly by sight,'' but only when she is moving. In lycosids, accordingly, there is no courtship or else a complicated one; sex recognition is by touch alone, or by touch and sight combined.

For the attids we have a considerable number of observations. Seidel (1847) states that at the time of mating several females of *Salticus scenicus* Hahn seek out one male and live with him. But the greater part of our knowledge on this group is due to the Peckhams. In 1889 they described the courtship of *Saitis, Epiblemum, Icius, Hasarius, Synageles, Marptusa, Phidippus, Dendryphantes, Zygoballus, Habrocestrum, Philaeus* and *Astia*, with full delineations, accompanied by excellent drawings, of the posturings and movements of the male, which in some species are the most complex yet known. There are peculiar jumping and wheeling movements constituting dances, besides erection and display of those parts of the body that are strikingly colored and modified. We have not space here to repeat their descriptions and could not, indeed, do justice to them in a short summary; the reader should refer to the original memoir. In a following paper (1890) these authors describe the courtship of *Habrocestrum*, which is peculiar in that a male exhibits an ornamentation of the third pair of legs, and they give new figures of the attitudes of *Synageles picata*.

In their last study (1909) they figure the male posturings in *Pellenes* and *Euophrys*—in *E. monadnock* the male taking such a pose as to display at once the yellow palps, the heavily bristled, black first leg pairs (held elevated), and the orange femora of the third and fourth pairs.

Finally, I would add the observations made by me last summer on a considerable number of pairs of the large *Phidippus purpuratus* C. Koch. Here the male is not much smaller than his mate, but much darker and with more iridescence. A male will court on sight of a female, without first touching her; his motions consist of elevation of the cephalic region, raising and outspreading the first leg pair (with some waving of them), accompanied with advance towards the female and retreat from her as well, as side-stepping. After a male has once courted and won a mate, if he is kept in the same cage with her, he thereafter courts to much less degree, and finally not at all, before embracing her; that is, he would seem to have lost his fear of her, and indeed the pregnant female will more frequently run away from him than he from her.

IV. INTERPRETATION OF THE COURTSHIP PHENOMENA

Preliminaries to mating, whereby one individual seeks to gain the favor of another, constitute what we mean here as courtship. My previous definition (1903) of it, "a rhythmically repeated set of motions on the part of the male," was incomplete in limiting the process to one sex, for the female also may take part. Some mode of courtship would then occur where there is no immediate seizure of the female by the male, and where one of the individuals, generally the male, is the more eager.

In some cases there is no courtship, where the male is as large or larger than the female, the male seizing the female—sometimes appropriating her when immature, and mating with her shortly after her last moult. And in the thomisids the male captures his mate by superior agility. But more usually there is some form of courtship, and this may be by either touch or sight.

In the case of courtship by touch, the simplest form, in Drassids, *Dictyna* and some Agelenids, is that where the male after recognizing a female by touch taps her rapidly with his feet until she either runs from him or else becomes quiet and submissive to his embrace. The more complex form is found among the snare-makers, especially epeirids and theridiids, and the courtship is by signal pulls upon the lines of the snare; in this way the male not only locates the position of the female upon her snare, but he also ascertains whether she is eager for him, for when she is eager she returns his signals in the same way.

Courtship by sight is found most highly developed in the attids, less complicated in the more corpuscular lycosids, but not at all in the diurnal thomisids; it is not, accordingly, characteristic of all diurnal species. The courtship movements of the male range from a simple waving of the first leg pair, or waving of these and the palpi, to much more complicated movements of these parts associated with peculiar posturings, advances and retreats, and side-wheeling.

This brings us to the important question, just what psychical and physiological elements enter into the courtship? We can most clearly discuss this by considering the sexes in turn. Without question the chief psychical condition is sexual desire, in the case of the male, resulting from a physiological state due to internal secretions at the time of maturity. But with it is associated an inhibiting factor, the male's fear of the female. When the male is as strong as the female he exhibits no special fear of her, she is rather distinctly timorous towards him, then he does not court but seizes her by force. But in most species the male is smaller, in some cases very much smaller, than the female, and in all such instances he indicates great caution in approaching her, which is a demonstration of fear on his part. Adult females are decidedly more pugnacious than males, and contests between females are generally fatal to one of the contestants, while this is seldom the result in battles between males. I once saw a male of *Phidippus purpuratus* kill his mature mate, and McCook (1890) has listed such cases in agelenids; but such happenings are very rare, and occur only when the male is as powerful as the female. In the great majority of species the male is decidedly afraid of the mature female, at least until after he has mated with her, and he does not exhibit towards her those aggressive movements which she often displays towards him. His embrace need not mollify her, for in certain epeirids and lycosids she has been seen to kill him immediately after the mating. It is interesting to note that one of the most general motions made by the male in courtship is the raising and extension of the forelegs towards the female, which is but a modification of a spider's general attitude of defense—a motion exhibited by both sexes when strongly disturbed.

Now there is courtship by the male only when he does exhibit this fear. Accordingly, we may conclude that courtship by the male spider results from a combination of the state of desire for and fear of the female. This explains satisfactorily why in some cases there is courtship while in other cases there is not. Courtship by the male continues until he has learned that the female is not hostile towards him; and his successive advance and retreat in her direction gives him the opportunity of experiencing, so learning, her degree of aggressiveness. By this courtship he advertises himself as a male, for no female shows such movements; and he may at the same time prominently display his ornamentation.

But we have neither reason to suppose that he is concious of influencing the female thereby, nor that he is conscious of exhibiting particular personal attractions towards her. For in those lycosids where there is little secondary sexual difference the male may have as complex courtship movements as in cases where he is more ornamental. And it is assuming too much about a spider's mentation to postulate that the male is not only conscious of his beauties, which are generally so placed that he can not perceive them himself, but has also an idea that he may arouse the female's esthetic sense. The Peckhams remark (1890, p. 122):

> That whatever fine points of color or structure the male possesses, his actions before the female display them to the very best advantage; indeed, he *seems* to have a strong consciousness of every advantage, and to sedulously strive to bring it to the notice and impress its beauty upon the mind of the female to whom he is paying his addresses.

But they add a modifying foot-note:

> We do not say that, in our opinion, he *is* conscious of his strong points. It is quite conceivable that the tendency to perform the antics may have developed along with the beauties which they serve to display without any idea of this existence dawning in the mind of the spider.

I think we should, until we have evidence to the contrary, accept as the correct interpretation the suggestion stated in that last sentence of the Peckhams, *i. e.,* that the male is not conscious that he is influencing the female, either sexually or esthetically.

We have just seen that the raising of the forelegs in courtship is but a modification of the general attitude of defense, therefore not primarily for display. The waving of the palpi may follow any excitement, is also not exclusively sexual. And I have been interested in finding a partial explanation of a male attitude exhibited by certain attids, namely the lateral flexion of the abdomen. In *Phidippus purpuratus* the male at frequent intervals in his courtship touches his spinnerets to the ground, thus attaching a silken line, and then in his side-wheeling before the female, with closed spinnerets, this line pulls his abdomen to one side. Such flexion of the abdomen, at least in this particular species, is thus not a conscious effort of display, but is due to a simple tension of the ordinary drag-line.

Last summer I observed in several species the curious phenomenon of males courting one another in the same way as they do females. I placed in a small cage two males of *Pardosa pallida,* Emert., and they moved their fore-legs and palpi just as in normal courtship. Two males, a smaller and a larger, of *Phidippus purpuratus* were placed together; the larger was aggressive, the smaller exhibited towards him normal courtship motions. In neither of these cases were females present. Two males of the brilliant *Phidippus mccookii* Peck. on being placed in one cage, on several different occasions, raised the legs, side-wheeled, and flexed the abdomen laterally, resembling a courtship; I had no female of this species to determine the normal courtship, but to females of *P. clarus* Koch they acted in the same way. Two males of *Zygoballus bettini* Peck. were placed in a cage and watched each other attentively, but without courtship; an immature female was introduced, when each male proceeded to court her: advancing and retreating by short quick steps, the first legs raised vertically and parallel and these and the palpi twitching; the female ran away from both, and after I had removed her the males exhibited the same movements towards each other, with the only difference that the raised legs were somewhat divergent and that the smaller male fled when the larger came too near. Evidently in these cases the males mistook one another for females, which would indicate that their visual discrimination is far from precise—perhaps less than that of the females.

The female is also actuated by sexual desire, sometimes quite as strongly as the male; this is the case with *Theridium tepidariorum,* where the female seems insatiable, and the Peckhams (1889) observed a female of *Saitis pulex* approaching a male with courting movements. In theridiids and epeirids the female signals along the snare lines quite as vigorously as the male does.

But whenever she is larger than the male, she exhibits as a rule, no great fear of him. She may express her desire to the male by remaining quiet and passive, or by touching him gently or moving towards him, or by counter-signalling by means of lines of her snare; and sometimes she may take the initiative in this. Where the courtship is by touch it is wholly excluded that the female can have any esthetic appreciation of the male, she is actuated either by sexual desire or by its absence. But where there is courtship by sight, as in the attids and some lycosids, the Peckhams have consistently maintained that the female is influenced by an esthetic appreciation of the colors, ornaments and postures of the male, and that she chooses that male that pleases her esthetic sense; and they have reiterated this view in their last paper (1909) without referring to my quite different interpretation (1903). Now there is no doubt that, as the Peckhams have shown, when there is courtship by sight the female attentively watches the male, and also no doubt that the male's motions are generally such as to exhibit his colors and ornaments to the best advantage; an exception to this is that the male of *Lycosa bilineata* exhibits no courtship although his fore-legs are provided with thick brushes of hairs. Then there is the interesting observation (Peckham, 1889) that of the two male forms of *Astia vittata* the female always selects the more ornamented *niger*-variety, which is darker and possesses plumose tufts on the cephalothorax, though it is not stated in how many cases this was observed. But it is significant that the *niger*-form "is much the more lively form of the two"; it might then be the case that the female selects him not because he is more ornamented, but because he is more lively,—therefore because he more quickly advertises himself as a male. This seems to me to be the correct understanding of the matter. For just as we have no evidence that the male consciously endeavors to exhibit his attractions, we have also no evidence that the female is influenced esthetically. What we do know is that the male by his courtship, a set of motions resulting from the conflicting states of sexual desire and fear, exhibits or advertises himself as a male; and that the female on sight of this courtship recognizes him as a male and accepts him if she be eager, or else becomes gradually stimulated by watching him. In other words, too great an assumption is made in supposing the female to have an esthetic sense, while it is more probable that the female is attracted by maleness alone and not by beauty. The immediate effect of courtship on the female is the stimulation of her sexual desire by recognition of a male, not first the arousing of an esthetic sense and second the arousing of sexual feelings. On my interpretation the case in *Astia* may be explained simply and without assumption: the *niger*-form is selected by the female because he is more different in color and structure from her than is the other male form, consequently is more quickly recognized as a male; this is what determines her, and not color or ornaments. The significance of peculiarities in color, structure and movements of the male lies in insuring quick sex-recognition, not in arousing esthetic feelings. The case of *Astia* is the only one known in which the female seems to exert a choice between males, dimorphism of males being rare in spiders.

We conclude, accordingly, that the male in visual courtship is not actuated by a conscious effort to exhibit his peculiar beauties, and that the female does not select males by an esthetic sense. Courtship by the male results simply because fear is mingled with his desire; and probably the female will accept the first male who courts her, and makes himself recognized as a male, at the time when she is physiologically desirous. Sexual selection in the meaning of Darwin, accordingly, and in opposition to the views of the Peckhams, has probably played no part in the evolution of the secondary sexual differences of spiders.

V. THE NATURE AND USE OF THE SECONDARY SEXUAL DIFFERENCES

We are not concerned here with the question of the first origin of secondary sexual differences, *i. e.*, whether they have arisen as gradual fluctuations, as Darwin held for the most part, or from acquired traits becoming inherited on the view of Cunningham (1900), or from sudden mutations as Morgan (1903) has suggested, for there is no observational evidence from which we can reason. We have rather to consider their value to the species, what is their use, and the factors which have served to perpetuate them.

In the first place it will be convenient to name categorically the main classes of secondary sexual characters found in animals in general, and second to discuss the significance of those found in araneads.

Plate (1908) has furnished a useful tabulation of secondary sexual characters, devised mainly to show "what an enormous morphological field is comprised in this term." The following arrangement of such characters is simpler than his, though as comprehensive, and will be more convenient for our present discussion.

1. Weapons employed by males in their combats with one another.
2. Characters used for sexual recognition and sexual stimulation.
3. Characters of more immediate value in ensuring approximation of the sexes and copulation.
4. Characters of value in provision for and nurture of the progeny.
5. Characters due to habitudinal differences of the sexes.
6. Characters of value in protecting a particular sex against other species.

We may next determine how these six main groups of characters are represented in spiders.

1. The weapons employed by males in their fighting for the possession of females are readily explained, as Darwin did in the first part of his theory of sexual selection, as being perpetuated by a natural selection between males.

Such direct combats between males do not appear to occur among spiders, neither do the males possess peculiar weapons, unless peculiarly modified chelicera may be considered as weapons. Mature males when placed together will frequently fight, but the Peckhams (1889) in describing this in the case of an *Icius* conclude that the battles are probably sham affairs, rarely resulting disastrously, and "gotten up for the purpose of displaying before the females." There may be more fighting between males when females are present, though there is no good evidence on this matter; but we have no reason to suppose that the males consciously endeavor to exhibit their prowess any more than they consciously try to display their ornaments. Males of the attid *Icius palmarum* placed in small cages were not observed by me to fight, nor were males of *Phidippus mccookii* nor those of *Zygoballus bettini;* but fighting of males was noticed in *Ceratinopsis interpres, Geotrecha pinnata* and *Xysticus nervosus,* and in the last species a male would leave the back of a female to fight a rival. But, as the Peckhams found, no injuries result to the males from this fighting, therefore these are not serious combats, and only once have I seen a male kill another male of his species (in *Prosthesima atra*).

Male spiders also do not possess intimidation organs, which result when weapons become hypertrophied according to the views of Guenther (1909).

2. Characters for sexual recognition and stimulation may be subdivided according to the sense organs which they affect, as Jäger (1874) has indicated. As we have seen, the only senses concerned in the case of spiders seem to be those of touch and sight. It may be that certain of the tactile organs, probably certain of the jointed spines, may become more numerous or more specialized at maturity to aid in sexual recognition, but this point remains to be tested. But those secondary sexual characters of male spiders found only where there is courtship by sight, such as ornamental colors and structures, and posturings that display them, fall under this category. Such are the male differences, as the Peckhams have shown, in the chelicera, clypeus, palpi and legs, that is, "in those parts of the animal that are plainly in view when the male is paying court to the female." Thus the chelicera may be lengthened, curved or spinous; the clypeus may be heightened or bear prominences; the first pair of legs may be thickened or have tufts of hairs; and any or all of these parts may have conspicuous color

markings. These differences are so pronounced in the attids that in many cases the species is known only by one of the sexes. We have previously seen that conscious esthetic choice by the female probably does not account for such male characters, that they are, accordingly, probably not due to sexual selection. These characters of the males may be most readily explained as being conserved by simple natural selection. Peculiar male ornamentation would be selected because it insures quicker sex-recognition, therefore prompter mating. The male is thereby more surely accepted by the female, not selected by her in the sense of Darwin. The process is much more an announcement of sex by the male than a choice by the female, and results in the female accepting the sex rather than the individual. There is no reason to suppose the female spider is actuated esthetically, while we do know she is actuated sexually—in some cases quite as much as the male is. There is no need of calling in any other factor than natural selection.

Whether such ornamental male characters, which stimulate the visual sense of the female, subserve sex recognition rather than sex stimulation we are hardly able to decide in the absence of any thorough analysis of the psychical states of spiders. But probably a female would first have to recognize a male as a male before she became sexually aroused by him, and for this reason male ornamentation would seem to be primarily to insure sex-recognition rather than sex-stimulation.

In opposition to the views of Wallace (1889) the Peckhams (1890) have correctly argued that the ornamentation of male spiders is not due to any "higher degree of vitality" of the males, for the female seems to be in all respects fully as active as the male, and at maturity even more active. The same objection may be made against the concept of Geddes and Thomson (1897) with regard to differences of the sexes.

The Peckhams have found in the attids, in agreement with Darwin's conclusions for birds, that: (*a*) when the adult male is more conspicuous than the adult female, the young of both sexes more closely resemble the adult female; (*b*) when the adult female is more conspicuous than the adult male, the young of both sexes more closely resemble the adult male; and (*c*) when both adults are alike the young of both sexes resemble them.

3. Characters of value after the act of sex-recognition to insure efficient mating would seem to be various, and all probably perpetuated by natural selection. Such would be the relatively larger legs in the case of certain males, in so far as they serve to hold the female. Smaller size and greater agility of the male, not a frequent phenomenon in araneads, would also aid in the mating by enabling the male to move more quickly upon the snare of the female, and to escape more rapidly from her should she be aggressive.

4. Characters of value in providing for and nurturing the young are limited in spiders to the female, and are also perpetuated by natural selection. Such are the greater size of the abdomen to accommodate the eggs, and the gland whose function is to agglutinate them. Such is also the greater pugnacity and bravery of the female, which is probably the expression of her greater need of food.

5. Characters due to habitudinal sex differences are few in spiders. Such differences first become marked at maturity, as do the other secondary sexual characters, all being in some way connected with internal secretions formed during the elaboration of the genital products. In the epeirids, as shown by me (1908*b*), immature males have the same mode of life as their sisters, and "construct perfect snares of the types of those of their respective females. But the adult males . . . do not spin snares at all, but build nests near those of adult females." Indeed, it is quite general among snare-making species that adult eager males regularly leave their snares to live upon or near those of females; and adult males of lycosids and drassids, which make no snares, leave their nests to seek for females. The chief habitudinal difference, accordingly, is that while the female continues a more or less

sedentary existence, or makes excursions mainly for food, the male in many species becomes a wanderer when he is adult, searching for a mate. The male thus comes to spin less and to run more; and a morphological consequence of this habit is seen in the total or nearly complete loss of the cribellum, or spinning plate, by adult males of certain species. It is possible his relatively greater leg length may be in some cases also associated with this habit. These few cases would fall in line with the theory of Cunningham (1900), being characters due to difference in mode of life of the sexes. But all such phenomena would be likewise regulated by natural selection.

6. The secondary sexual characters which operate to protect a particular sex in the struggle for existence are found mostly in the females, and these would be subservient to natural selection. In certain spiders, as notably some epeirids (*Argiope, Acrosoma, Gasteracantha*), the female is not only much larger than the male, but also much more brightly colored, often with most conspicuous black and yellow or red and yellow markings; and in *Acrosoma* and *Gasteracantha* the abdomen may be drawn out into angular processes and spines. We can not accept for this case the Peckhams' suggestion that this is due to difference of mode of life of the sexes, for so far as is known the males of these have the same mode of life as those of other epeirids. These brilliant and remarkable females all build their snares in the open sunshine, and remain upon the centers of the snares. They would seem rather to represent cases of warning coloration, this ultimately protective to the possessors: in *Acrosoma* and *Gasteracantha* the bright markings would serve to advertise the hard and spinous abdomina, and in *Argiope*, which is soft-bellied, perhaps to announce the large snare. Possibly the brushes of hairs on the legs of another female epeirid, *Nephila,* would be an example of warning characters calling attention to the unusually large and powerful web, thus protecting the snare against birds. It is always difficult to be sure of a correct interpretation of phenomena of this kind, but it would seem probable

that some cases of brighter female coloration represent examples of warning coloration, and consequently come under our sixth category of secondary sexual phenomena.

It will be recalled that Wallace (1889) explained the general less conspicuous coloration of female birds on the ground of their need of greater protection, since they play the major rôle in guarding the nest and the eggs. The Peckhams (1889) have argued that this idea would not apply to the general inconspicuous coloration of female attids, because when they have eggs they hide these and themselves within thick silken nests and so are sufficiently protected from enemies. But I believe Wallace's explanation will apply in the case of spiders. For the males do not develop their ornamentation until maturity, and they have much less need of protection than the females because they live usually not much longer than a few weeks after maturing, and take no part in the care of the young. The males have fulfilled their main function after impregnating the females, and they are of no use to the species thereafter. But the females live at least several months after maturing, in some cases several years, and they have the whole care of the eggs and young. In araneads, as in all animals, the females are of the greater importance in the perpetuation of the race. Therefore it is probable, in agreement with Wallace, that natural selection has generally maintained a more protective coloration of the female.

In all six categories of secondary sexual characters in so far as spiders are concerned, accordingly, natural selection alone is sufficient to explain the regulation of the phenomena. At the same time these phenomena would seem to have a manifold origin, as they certainly fulfill very different uses.

LITERATURE LIST.

1873. Canestrini. Caratteri sessuali secondarii degli Arachnidi. Atti Soc. Veneto-Trentina Sc. Nat. Padova. 1.

1900. Cunningham, J. T. Sexual Dimorphism in the Animal Kingdom. London.

1886. Darwin, C. The Descent of Man, and Selection in Relation to Sex. New ed., New York.

1878. Emerton, J. H. The Structure and Habits of Spiders. Salem.

1897. Geddes, P., and Thomson, J. A. The Evolution of Sex. London.

1909. Guenther, K. Der Kampf um das Weib in Tier- und Menschenentwicklung. Stuttgart.

1874. Jäger, G. In Sachen Darwins. Stuttgart.

1887. Lendl. Ueber die Begattung und die Copulationsorgane von Trochosa infernalis Motsch. Term. Füzetek. Budapest, 11.

1890. McCook, H. C. American Spiders and their Spinning work, Vol. II. Philadelphia.

1843. Menge, A. Ueber die Lebensweise der Arachniden. *Neueste Schr. naturf. Ges. Danzig*, 4.

1866. Menge, A. Preussische Spinnen. *I. Schr. naturf. Ges. Danzig* (N. F.), 1.

1872. Menge, A. *Idem*, 5. Ibid., 3.

1873. Menge, A. *Idem*, 6. Ibid.

1874. Menge, A. *Idem*, 7. Ibid.

1877. Menge, A. *Idem*, 10. Ibid., 4.

1903. Montgomery, T. H. Studies on the Habits of Spiders, particularly those of the Mating Period. *Proc. Acad. Nat. Sci. Philadelphia.*

1908*a*. Montgomery, T. H. The Sex Ratio and Cocooning Habits of an Aranead, and the Genesis of Sex Ratios. *Jour. Exper. Zool.* 5.

1908*b*. Montgomery, T. H. Further Studies on the Activities of Araneads. AMER. NAT., 42.

1903. Morgan T. H. Evolution and Adaptation. New York.

1889. Peckham, G. W. and E. G. Observations on Sexual Selection in Spiders of the Family Attidae. Occas. Papers Nat. Hist. Soc. Wisconsin, 1.

1890. Peckham, G. W. and E. G. Additional Observations on Sexual Selection in Spiders of the Family Attidæ. *Ibid.*, 2.

1909. Peckham, G. W. and E. G. Revision of the Attidæ of North America. *Trans. Wisconsin Acad.*, 16.

1907. Petrunkevitch, A. Studies in Adaptation. 1. The Sense of Sight in Spiders. *Journ. Exper. Zool.*, 5.

1908. Plate, L. Selectionsprinzip und Probleme der Artbildung. 3te Ausg., Leipzig.

1905. Pritchett, A. H. Observations on Hearing and Smell in Spiders. AMER. NAT., 38.

1847. Seidel. Einige Beobachtungen an Spinnen. Uebersicht Arbeit. Veränd. Schles. Ges. väterl. Kultur, Breslau.

1866. Termeyer, R. M. de. Researches and Experiments upon Silk from Spiders, and upon their Reproduction. *Transl. by B. G. Wilder. Proc. Essex Inst.*, 5.

1879. Treat, M. The Habits of a Tarantula. AMER. NAT., 13.

1888. Wagner, W. Des poiles nommés auditifs chez les Araignées. *Bull. Soc. Nat. Moscow.*

1837. Walckenaer. Histoire Naturelle des Inséctes, Aptères. Suites à Buffon, 2. Paris.

1889. Wallace, A. R. Darwinism. London.

1861. Westring, N. Araneæ Suecicæ descriptæ. Gothoburgi.

NOTES AND LITERATURE

NOTES ON ICHTHYOLOGY

One of the most important publications in ichthyology, as a result of the stimulus given to zoology by our knowledge of evolution, is the "Cave Vertebrates of America," by Dr. Carl H. Eigenmann, of the University of Indiana, published by the Carnegie Institution of Washington. In this large and finely printed volume is a complete discussion of caves and of cave fauna, the greater part of this fauna being composed of blind fishes. The caves of Indiana, Kentucky, Missouri and Cuba have been especially investigated in this paper. Dr. Eigenmann shows very conclusively that those species of fishes which are the ancestors of the blind forms were of those types which avoid the light, skulking in darkness in preference. Those fishes which take their prey by sight alone are never represented among the ancestors of cave fishes. Dr. Eigenmann adopts the judgment, independently reached by Mr. Garman, that the originals of the cave species (non-aquatic, especially) of Kentucky were probably already adjusted to a life in the earth before the caves were formed. Dr. Eigenmann concludes:

1. That the cave fauna is in large part the result of this formation of the caves themselves, that environment and habitat developed *pari passu.*

2. That to this original fauna have been added and are being added species (such as *Spelerpes maculicauda*) which, because they are negatively heliotropic or positively stereotropic, are gradually becoming adapted to the deeper and deeper recesses of caves.

3. That to the fauna of the larger caves may also have been added animals which had become adjusted to cave existence in crevices, under banks or rocks, etc., that is, in small caves.

4. That accident has played little or no part in developing the cave fauna.

As to the general cause of degeneration, Dr. Eigenmann is inclined to take the Lamarckian view, involving the inheritance of results of disuse. A number of species of blind lizards are discussed, as well as certain blind fishes which are not found in caves. Among these are the parasitic hag fishes, *Polistotrema stouti,* of the coast of California, and the blind goby of Point Loma, in California, *Typhlogobius,* which lives in the darkness on the under side of shelving rocks. There is also a blind catfish, *Ameiurus nigrilabris*, which is found in caves of Lancaster County, Pennsylvania.

The best known of the blind fishes belong to the family of Amblyopsidæ. The genus, *Chologaster*, contains one species with eyes, inhabiting the channels about the Dismal Swamp and the rice canals of the South. The other species are known only from caves and cave springs, and all the representatives of the genera, *Amblyopsis*, *Troglichthys* and *Typhlichthys*, are blind.

Dr. Eigenmann has also made an elaborate study of the blind fishes of Cuba, *Lucifuga subterranea* and *Stygicola dentatus*. These two fishes belong to the family of Brotulidæ, a relative of the blennies. The origin of these forms is from marine fishes living in clefts of coral rock. This coral rock, when raised above the sea, seems to have carried these forms with it. The nearest related genus, *Brosmophycis*, still lives among the corals.

The details of anatomy, as well as the details of environment, of each of these species, are very fully illustrated in this paper, which is by far the most important one yet devoted to this subject.

Dr. Eigenmann observes in conclusion that it is absolutely certain that the caves were not peopled by a catastrophe, and, further:

> That the cessation of use was gradual and the cessation of selection must also have been a gradual process. There must have been ever widening bounds within which the variation of the eye would not subject the possessor to elimination.
>
> *Chologaster* is in a stage of panmixia as far as the eye is concerned. It is true the eye is still functional, but that the fish can do without its use is evident by its general habit and by the fact that it sometimes lives in caves.
>
> The present conditions have apparently existed for many generations, as long as the present habits have existed, and yet the eye still maintains a higher degree of structure than reversed selection, if operative, would lead us to expect, and a lower degree than the birth mean of fishes depending on their eyes—the condition that the state of panmixia alone would lead us to expect. There is a staying quality about the eye with the degeneration, and this can only be explained by the degree of use to which the eye is subjected.
>
> The results in *Chologaster* are due to panmixia and the limited degree of use to which the eye is put. *Chologaster agassizii* shows the rapid diminution of the eye with total disuse.
>
> The difference in the conditions between *Chologaster* and *Amblyopsis*, *Typhlichthys* and *Troglichthys* is that in the former the eyes

are still in use, except when living in caves; in the latter they have not been in a position to be used for hundreds of generations. The transition between conditions of possible use and absolute disuse may have been rapid with each individual after permanently entering a cave. Panmixia, as regards the minute eye, continued. Reversed selection was inoperative, for economy can not have affected the eye for reasons already stated. Simply the loss of the force of heredity, unless this was caused by disuse or the process of germinal selection, can not have brought about the conditions, because some parts have been affected more than others.

Considering the parts most affected and the parts least affected, the degree of use is the only cause capable of explaining the conditions. Those parts most active during use are the ones reduced most, viz., the muscles, the retina, optic nerve and dioptric appliances, the lens and vitreous parts. Those organs occupying a more passive position, the scleral cartilages, have been much less affected and the bony orbit least. The lens is one of the latest organs affected, and not at all during use, possibly because during use it would continually be in use. It disappears most rapidly after the beginning of absolute disuse both ontogenetically and phylogenetically. All indications point to use and disuse as the effective agent in molding the eye. The process does not, however, give results with mathematical precision. In *Typhlichthys subterraneus* the pigmented layer is affected differently from that of *Amblyopsis*. The variable development of the eye muscles in different species would offer another objection if we did not know of the variable condition of these structures in different individuals. Chilton has objected to the application of the Lamarckian factor to explain degeneration on account of the variable effects of degeneration in various invertebrates. But such differences in the reaction are still less explicable by any of the other theories.

In the *Biological Bulletin* for January, 1905, Professor Eigenmann describes two species of blind fishes, *Typhlichthys osborni*, from Horse Cave, Kentucky, and *Typhlichthys wyandotte*, from Corydon, Indiana, near the large Wyandotte Cave.

In the Field Columbian Museum, February, 1909, Dr. Seth E. Meek describes a number of species from Tropical America. These are: *Rhamdia nasuta*, from Buenos Aires de Terraba, Costa Rica; *Astyanax regani*, from Las Cañas, Costa Rica; *Cyprinodon dearborni*, from Willemstad, Curaçao, Dutch West Indies; *Girardinus vandepolli*, from Curaçao; *Pœcilia caudata*, from Turrubares, Costa Rica; *Cichlasoma punctatum*, from Buenos Aires de Terraba, Costa Rica; and *Cichlasoma frontale*, from Turrubares, Costa Rica.

In the *Proceedings of the Zoological Society of London*, 1909, Mr. Regan describes a collection of fishes from Christmas Island, six species being new.

In the same *Proceedings,* 1909, Mr. Regan gives an interesting account of the changes in coloration in living fishes, as observed in the New York Aquarium. The same subject has been since much more fully treated by Charles H. Townsend, director of the aquarium.

In the *Annals and Magazine of Natural History,* 1909, Mr. Regan gives the name *Orectolobus ogilbyi* to the species from Torres Straits which Ogilby and McCulloch had identified with *Orectolobus dasypogon.* Mr. Regan admits that *Eucrossorhinus,* established by him for *dasypogon,* is not distinct from *Orectolobus.*

In a publication of the Station at Boulogne-sur-mer, Dr. H. E. Sauvage gives a comparative study of the peritoneum of flounders.

In the *Bulletin de la Société Belge de Géologie,* 1908, Mr. Maurice Leriche discusses new species of fishes from the Oligocene of Belgium.

In the *Annales de la Société Géologique du Nord,* Volume 37, 1908, at Lille, Mr. Maurice Leriche discusses the fossil sharks of California, with special reference to the papers of Agassiz and Jordan. Leriche regards these American species as identical with the nearest corresponding species of Europe. It is a matter in which certainty is not often possible. Most of the living species now found on the Pacific Coast are different from the corresponding living sharks of Europe, but this is apparently not true in every case, and in most cases the teeth do not show adequate differences. It is also not possible in every case to know whether different teeth represent really different species, or whether they may be from different parts of the mouth of the same animal. *Heptranchias andersoni,* from California, is identified with *Notidanus primigenius,* of Agassiz. It may be here noted that *Heptranchias* of Rafinesque is much the older of the two generic names concerned. *Lamna clavata,* of Agassiz, is identified with the European *Lamna cuspidata,* of Agassiz. Mr. Leriche states that in another paper he will show that this species belongs to *Odontaspis,* and not to *Lamna.* Mr. Leriche regards *Isurus planus, I. tumulus* of Agassiz, and *I. smithii* of Jordan, as identical. *Planus,* according to Leriche, represents the upper teeth, and *tumulus* the lower teeth, while *smithii* is the name of the front teeth of young specimens. It is not unlikely that this view of the case is the correct one. We may notice, however, that Rafinesque's name *Isurus* is much older than *Oxyrhina*. *Carcharodon rectus,* of Agassiz, and *C. branneri,* of Jordan, are regarded as identical with *C. megalodon,* the giant shark of the Miocene fossil beds about the Atlantic. *C. arnoldi,* of Jordan, and *C. riversi,* of Jordan, Leriche regards as identical with the living *C. rondeleti,* for which the older name is *C. carcharias.* This may possibly be true of the *riversi,* but the *arnoldi* is based on a specimen far larger than that of the largest living man-eating shark, *C. carcharias. Hemipristis heteropleurus,* of Agassiz, is regarded as identical with the European *Hemipristis serra.* This identity was also indicated by Dr. Jordan. *Galeocerdo productus,* Agassiz, is regarded as identical with *G. aduncus,* Agassiz. Among the unidentified teeth photographed in Jordan's paper, Leriche recognizes *Aprionodon, Galeus* and *Squatina.*

Leriche also notes that these observations show the great geographical extension of the species of sharks, and the importance that these have in the establishment of synchronisms at great distances. It is, however, true that specific differences of many kinds exist in species of shark, without showing themselves in the teeth. It is, however, safe to recognize no species as now known by the teeth alone, unless the teeth show tangible differences.

In the same annals Leriche describes numerous sharks and other fishes from the early Tertiary about Rheims.

In the same annals Leriche describes the teeth of various carboniferous fishes of the north of France and of Belgium.

In *Science*, May 28, 1909, Mr. Barton A. Bean shows that the name of the American eel should be *Anguilla rostrata* (Le Sueur), this name being earlier than that of *chrisypa* given by Rafinesque at about the same time.

In the *Bulletin of the American Museum of Natural History,* Volume 26, 1909, Dr. L. Hussakof describes a new species of the extraordinary genus of goblin sharks, of which the living form is known as *Mitsukurina,* and the extinct species by the earlier name of *Scapanorhynchus.* Dr. Hussakof gives to this new species the name of *Scapanorhynchus jordani.* In this species, the long blade of the snout is longer than in *S. owstoni;* the eye is further forward, the gills are smaller, and there are other differences of importance. Dr. Hussakof has no doubt that *Mitsukurina* is identical with the Cretaceous *Scapano-*

rhynchus, as indicated by Dr. Woodward. The differences between these living and fossil species are no greater than the differences among the species of the genus itself. Dr. Hussakof agrees with Jordan that *Scapanorhynchus* is closely related to the Odontaspid sharks, but whether it should be placed in that family or constitute a distinct family must depend on further studies of its anatomy.

One of the most remarkable features in geographical distribution is the extraordinary number of singular animals, especially sharks and chimæras, which have been discovered in the waters of Sagami Bay, the first bay to the southward of Tokyo in Japan.

In the Mark Anniversary Volume Dr. Jacob Reighard describes in great detail the natural history of the bowfin, *Amia calva,* with colored plates of different stages in the development of this singular fish.

In the *Proceedings of the Biological Society of Washington,* 1909, Dr. Barton Warren Evermann and Edmund Lee Goldsborough describe a number of fishes from the canal zone of Panama. Of these, *Cheirodon gorgonæ,* from Gorgona, is new.

In the same *Proceedings,* 1909, Dr. Barton Warren Evermann and John Treadwell Nicholas describe the fishes of Crab Creek, in the state of Washington, and with a new species or variation of trout known as *Salmo eremogenes.* This is a very robust form, with the spots gathered on the posterior part of the body. It is apparently a variant of the cut-throat trout, *Salmo clarki.*

In the same *Proceedings,* 1909, Dr. Evermann and Lewis Radcliffe have an interesting note on *Orestias agassizii,* a singular fish from Lake Titicaca.

In the *Memoirs of the Carnegie Museum,* Volume 4, 1909, Dr. Jordan and Robert Earl Richardson have a catalogue of the fishes of the island of Formosa, or Taiwan, based on the collections of Dr. Hans Sauter. The fauna of this island is essentially tropical, and intermediate between that of Japan and that of India. Most of the two hundred and eighty-six species known are from sandy shores and bays, scarcely any collections having been made among the coral reefs. In this paper nine new species are described and elegantly figured.

In the *Annals of the Carnegie Museum,* Volume 6, 1909, are three reports of the expedition to British Guiana of the Indiana University and the Carnegie Museum. This is part of the work undertaken by Dr. Carl H. Eigenmann under the joint patronage of the two institutions mentioned, and having in view as its final purpose a complete investigation of the geographical distribution of fresh water fishes in South America, and the relation of the barriers separating river basins to the development of new species. The first of these reports by Dr. Eigenmann gives new genera and species of fishes in British Guiana. A remarkable feature of this investigation is the discovery that almost all types of fishes found in different species in North America are represented in South America by analogies belonging to the family of Characidæ. Thus, minnows, chubs, suckers, darters and perches all have their representatives in a family which is not represented by any of these, but which practically monopolizes the waters of South America.

The second of these reports, by Marion Lee Durbin, describes one new genus and twelve new species of characins.

In the third report, Mr. Christian B. Blosser describes fishes obtained, most of them incidentally, in the West Indies and on the coast of Guiana. The following are new species: *Apogonichthys melampodus,* from St. Croix; *Bodianus stellatus,* from St. Croix; *Holocanthus lunatus,* of St. Croix; *Spheroides asterias,* St. Croix. *Chromis marginatus,* a species not previously found so far north, was also found at St. Croix.

In the *Proceedings of the Royal Society of New South Wales,* 1908, Ogilby and McCulloch offer a revision of the Australian Oretolobidæ, group of carpet-sharks, some of them known locally as wobbegongs.

In the *Records of the Australian Museum,* Allan R. McCulloch publishes studies in Australian fishes, No. 2, with descriptions of a number of new or rare species from about Sydney.

In the *Ann. Mus. Zool.* of St. Petersburg, Volume 14, 1909, Dr. Leo S. Berg demonstrates the distinctness of the genus *Acanthogobio* from *Hemibarbus.*

In the same publication, Dr. Berg discusses the trout of the Sea of Aral, *Salmo trutta aralensis.*

In the same bulletin, Dr. Berg discusses the salmon of the Black Sea, *Salmo salar labrax.*

In the same bulletin Dr. Berg gives a list of the fishes of the River Ob, or Obi, forty-two in number.

In a publication of the Provincial Museum of Natural History and Ethnology, at Victoria, British Columbia, 1909, Mr. Francis Kermode, curator, gives a list of the animals represented in the collection, with excellent photographs of many of the species of fish, as well as of birds, totem poles and other objects of interest. This collection has the only two known specimens of the prow fish, *Zaprora silenus.*

In the *Proceedings of the Biological Society of Washington,* Volume 22, 1909, Mr. T. D. A. Cockerell, of the University of Colorado, with Mr. Otis Callaway, has a very interesting discussion of the scales of fishes, as showing their genetic relationship. In this paper the herbivorous cyprinoid fishes are treated, and it is shown that the subfamily Chondrostominæ, as recognized in America, is even more heterogeneous than was hitherto supposed. *Chrosomus* stands entirely apart from the others, its scales having the primitive sculpture of the scales of the suckers. The herbivorous forms in America are divided by Mr. Cockerell into four subfamilies: Chrosominæ, including *Chrosomus;* Chondrostominæ, including *Acrocheilus* and *Orthodon;* Campostominæ, including *Campostoma;* and Pimephalinæ, including *Pimephales* and *Hybognathus.* These last are most nearly related to the ordinary minnows.

In the same *Proceedings*, 1909, Mr. Cockerell, and Miss Edith M. Allison, continue the investigations of the scales of fishes, with photographs of several of the different types. Taking up the genus called *Leuciscus,* he suggests that probably none of this species are congeneric with the European *Leuciscus leuciscus.* If this view is correct, which seems probable, the name *Richardsonius* should probably be adopted for the American forms referred to this group. *Lavinia* is not one of the Chondrostominæ, but it is closely related to the forms called *Richardsonius.* Probably none of the American species referred to the genus *Rutilus* of Rafinesque are congeneric with the *Rutilus rutilus* which is an ally of *Leuciscus.* Mr. Cockerell separates *Nocomis,* of which the type is *kentuckiensis*, from the genus *Hybopsis,* basing the genus on the character of the scales. These are supported by numerous minor characters. *Hybopsis gelidus* is made by Cockerell the type of a new subgenus, *Macrhybopsis.* Cockerell regards *Hybopsis, Notropsis* and *Cliola* as derived from Pimephalinæ.

These investigations of the character of the scales seem likely to prove very important as indicating the real relationships of these variant forms.

In the *Bulletin of the Museum of Comparative Zoology*, 1909, Mr. Henry B. Bigelow describes the cruise of the United States Fisheries Schooner "Grampus" in the Gulf Stream during July, 1908.

In the *Proceedings of the United States National Museum,* Volume 37, 1909, Professor Oliver P. Hay, discusses the nature of the fossil sharks, with tooth-like structures, known as *Edestus,* with a description of a new species and a new genus, *Toxoprion.* Dr. Hay regards these, not as teeth, but as a succession of spines or spinal structures in front of the dorsal fin, and used as weapons of offense.

In the *Proceedings of the National Museum,* Volume 36, 1909, Professor John O. Snyder describes new genera and species of fishes obtained on the voyage of the "Albatross," in 1906, on the Coast of Japan and the Riu Kiu Islands.

In the Smithsonian Miscellaneous Collections, Volume 52, 1909, Barton A. Bean and Alfred C. Weed discusses the life history of the Alaskan fresh-water sculpin, *Cottus asper.* These little fishes are extremely greedy and destroy great numbers of salmon eggs.

The British Museum has published the first volume of an elaborate catalogue of the fresh-water fishes of Africa, by Dr. George Albert Boulenger. The first volume contains the Mormyridæ, the Characinidæ, and part of the Cyprinidæ, with a number of minor families. The book is well printed, and each of the species is represented by a good plate.

In *Zoologica,* for 1909, Mr. Edward Phelps Allis, Jr., publishes a most elaborate account of the anatomy of certain mail-cheeked fishes, fifteen species being represented in his studies, and the bony structure of each of these described with a degree of fullness not hitherto shown in any papers on the osteology of fishes. This piece of work is accompanied by admirable engravings. The only suggestion which could arise by way of criticism is that not nearly all the types of the mail-cheeked fishes are represented, and that a full comparative study in which all of them would be considered might lead to results which can not flow from merely descriptive work on a part of a large and varied group.

In the Publications of the Department of Fisheries of New South Wales, for 1908, David G. Stead discusses the beaked salmon, *Gonorhynchus,* and its distribution in Australia.

In the same publications, Mr. Stead describes a number of new species of fish from the coasts of New South Wales.

In the *Annals of Queensland Museum,* Number 9, for 1908, Mr. J. Douglas Ogilby describes a number of new species and genera from the coast of Queensland.

In a second paper Mr. Ogilby discusses the toad-fishes of Queensland. A new genus, *Batrachomœus,* is proposed for *Batrachomœus minor,* and a new genus, *Coryzichthys,* for *Batrachoides diemensis.* This differs from the American genus, *Marcgravia,* in a much smaller number of fin rays. A new generic name, *Halobatrachus,* is proposed for *didactylus* of the Mediterranean. This differs from *Batrachoides* in the presence of an axillary pore.

In the index to the meeting of the British Association for the Advancement of Science, at Winnipeg, 1909, Professor W. A. Herdman gives an interesting discourse on "Our Food from the Waters," the investigation of plankton being made especially prominent.

In the *Memoirs of the American Museum of Natural History,* Volume 9, 1909, Professor Bashford Dean presents studies on fossil fishes (sharks, chimæroids and arthrodires). This contains, among other things, an elaborate study of the genus *Cladoselache,* a Devonian shark, and one of the simplest, as well as the earliest, representatives of that group. Elaborate drawings are given of the structural characters of *Cladoselache,* and the final conclusion is that these represent better than any other the primitive shark. Dr. Dean agrees with Woodward that if the earliest true fish could be found, it would almost certainly fall within the subclass to which belong our modern sharks; and the fundamental characters of the cladoselachian have given us a less ghostly picture of a direct vertebrate ancestor.

As to the arthrodires, Dr. Dean thinks that the present evidence does not lead us to affirm that these fishes possessed paired appendages homologous with pectoral and pelvic fins. There is still, therefore, a great gap remaining between these forms and the true fishes.

In the *Bulletin of the United States Geological Survey,* Mr. Earle Bernard Phelps discusses the subject of the pollution of streams by sulphite pulp waste. The exclusion of these forms of waste from the streams is one exceedingly important in the protection of the fishes of our rivers. Thus far, it has not been possible to prevent the flow of these mischievous substances into the streams, and their value for utilization in other ways is very slight. According to Mr. Phelps, the best promise seems to be along the line of the formation from sulphite of the dye called "lignone." These substances dye wool directly, giving brilliant yellow, brown and green colors that are fast to soap, acids and alkalies, and reasonably fast to sunlight.

In the Report of the Commissioner of Fisheries of British Columbia, 1908, Mr. John Pease Babcock, Commissioner, discusses the salmon problems of Puget Sound, and the Treaty of April 11, 1908, under which the International Fisheries Commission has been organized.

In the *Comptes Rendus* of the Academy of Sciences of Paris, M. A. Cligny describes a new genus of Zeinæ, called *Parazenopsis,* from Morocco. The species is *Parazenopsis argenteus.*

In the *Annales de la Station Aquicole de Boulogne-sur-Mer,* M. Cligny shows that the species called *Harengula latulus* is nothing but a common sprat, *Clupea sprattus.* The species called *Meletta phalerica* and *M. mediterranea* are also identical with the common sprat, the Mediterranean representatives of which form a geographical race, distinguished from the races in the north of Europe, having one less vertebra, and a few less of the anterior rays.

In the same *Annales,* M. Cligny discusses the genus of *Scorpœnidœ* called *Helicolenus.* He shows that three distinct species have been confounded under the name of *maderensis.* Of these, the first, that of Cuvier, should disappear, being a simple variety of *Scorpœna scrofa;* the second, that of Lowe, should receive a new name; the third, that of Goode and Bean, should disappear, being a synonym of *Helicolenus dactylopterus.* M. Cligny, however, conscientiously refrains from giving this new species a distinctive name, because he has never had any specimen in hand.

> Nous ne nous permettons pas de donner un nom nouveau à une espèce que nous n'avons jamais eue sous les yeux; nous laissons ce soin à un naturaliste plus favorisé et qui pourrait donner en même temps un diagnose précise de l'espèce.

In the same *Annales,* M. Cligny discusses in greater detail the new genus *Parazenopsis.*

In Notes from the Leyden Museum, Volume XXXI., 1909, Professor Max Weber, of Amsterdam, describes new fishes obtained by the Siboga Expedition to New Guinea and neighboring waters. A number of new species are added to the endlessly rich fauna of the Island of the Tropical Pacific. *Rhabdamia* and *Siphamia* are new genera related to *Apogon.*

In another paper, in connection with the aquarium at Amsterdam, Dr. Weber adds a new *Fierasfer* to the list of Siboga fishes.

In the AMERICAN NATURALIST, Vol. 42, 1908, Professor Cockerell describes the results of the expedition to Florissant in 1908. In this wonderful deposit of fossils, specimens of *Trichophanes foliarum*, of Cope, were found. This little fish, of which figures are given by Professor Cockerell, appears to belong to the suborder Xenarchi, and to be a near relative of *Aphredoderus*, a living pirate perch. It shows also relationships with the trout perch, *Percopsis*, like *Aphredoderus*, a relic of a waning fauna.

In the *Records of the Canterbury Museum*, Volume 1, 1909, Mr. Edgar R. Waite gives an account of the scientific results of the New Zealand Government Trawling Expedition of 1907. A number of new species are described, one of the most interesting being the blind torpedo, *Typhlonarke aysoni*. Only the sharks and rays are discussed in this first paper.

Under the head of "Salmon Scales as Indicative of the Life History of the Fish," Mr. J. Arthur Hutton publishes, in the form of a paper read before the Manchester Anglers Association, an article in which he shows that the scales of salmon are obtained through life, and that in a general way the age of the fish can be shown by the scales. During its stay in fresh water, the scales rapidly disintegrate, and are restored again when the fish returns to the sea. In his judgment the European salmon does not live over eight or nine years. Mr. Hutton illustrates his thesis by numerous photographs of salmon scales.

In the *Memoirs of the Indian Museum*, Volume 2, Dr. N. Annandale, the superintendent of the museum, commences a report of the fishes taken by the Bengal Fisheries Steamer "Golden Crown." The first paper treats solely of the rays, of which numerous species were obtained. One partially blind torpedo is given the name *Bengalichthys*.

In the *American Journal of Obstetrics*, Dr. Charles R. Stockard discusses the formation of cyclopean monsters among fishes by bringing up the little fishes in solutions of sea water containing chloride or nitrate of magnesium.

The same subject is discussed by Dr. Stockard in the *Anatomical Record*, Volume 3, 1909.

In the *American Journal of Anatomy*, Volume 9, 1909, Dr. Harold D. Senior discusses the development of the heart in the shad, with descriptions and bibliographies.

In the *Anatomical Record*, Volume 1, 1907, Dr. Senior discusses a number of rows of valves in the arterial bulb in the heart in different fishes. In most bony fishes the arterial bulb contains a single tier of valves. In *Albula*, there are two tiers; in *Elops* one tier; in *Pterothrissus* two tiers.

In the *Philippine Journal of Sciences*, Volume 4, 1909, Mr. Alvin Seale discusses very fully the fishery resources of the Philippine Islands, with colored plates of a number of the more valuable species.

In the same *Journal*, Mr. Seale discusses the sponge fisheries of the Philippine Islands, with numerous plates.

In the *Biological Bulletin*, Mr. H. H. Newman, of the University of Texas, discusses hermaphroditism in fishes, a bisexual specimen of *Fundulus* being considered, this being a species in which the females are very differently marked from the males.

In the same *Bulletin*, Mr. Newman discusses the contact organs, fine papillæ found on the scales and fins in certain fishes. These have been studied by him in species of *Fundulus* at Woods Hole. These contact organs are supposed to give the fish greater sensitiveness, and also, perhaps, to increase the frictional surface of the animal.

In the *Journal of the College of Science in the Imperial University of Tokyo*, 1908, Mr. Shigeho Tanaka describes six species new to science from the East Coast of Japan.

In the same *Journal*, 1909, Mr. Tanaka describes eleven new species of Japanese fishes, one of them being a new genus of Chimæras called *Anteliochimæra*. This form has a snout produced in a long spatula, as in *Rhinochimæra*. It adds one more to the dozen or so extraordinary forms of sharks, skates and chimæras which have been obtained within the last ten years in the Bay of Sagami.

This specimen was caught, probably, with a hook, in a depth of four hundred fathoms, by the remarkable collector employed at the Seaside Laboratory at Misaki, Kuma Aoki. This unlettered fisherman, who can not read even his own language, is in his way one of the cleverest ichthyologists in Japan.

In the *Annotationes Zoologicæ Japonenses*, Volume 7, 1909, Mr. Tanaka discusses a collection of fishes from the interior province of Shinano.

In the *Proceedings of the United States National Museum*, 1909, Jordan and Richardson give a review of the sea bass, or Serranidæ, inhabiting the waters of Japan, with numerous figures, and the description of one new species. When this series of monographic reviews of Japanese fishes was begun, in 1900, as a result of the exploration made in that year by Jordan and Snyder, it was hoped that they would serve to furnish to Japanese naturalists a record of the literature largely inaccessible to them, and a record of descriptions of the known species. It was hoped at the same time that making the literature of the subject compact in this way would lead to a rapid development of the science of ichthyology among the Japanese naturalists themselves. The recent publications of Ishikawa, Kishinouye Otaki, and Tanaka, and of other students of the great teacher, Mitsukuri, have shown that these expectations have not been disappointed.

In the *Revista Universitaria*, Peru, 1909, Professor Carlos E. Porter, of Valparaiso, gives a list of the most important fishes on the coast of Chili and Peru. Forty-six species are enumerated.

In the Publications of the Bureau of Science of the Philippine Islands, at Manila, Jordan and Richardson give a check list of the fishes known to inhabit the waters of the Philippine Islands. This list, based on the various collections made under the auspices of the United States Government, and of the local Bureau of Science, now numbers eight hundred thirty species. It is probable that a full enumeration of the fishes of these islands will rise to double that number. One new genus is proposed in this paper, *Vespiculus* for *Prosopodasys gogorza*.

DAVID STARR JORDAN.

ENTOMOLOGY

A New Catalogue of Hemipterous Insects.[1]—A catalogue exhibits the taxonomy of a group in its most condensed form. For this reason, it is as interesting and valuable to a specialist as it is uninteresting and unintelligible to one who has paid no attention to the particular order or family it represents. It has indeed a very high value for the uninitiated, inasmuch as it gives him a clue to the literature on and affinities of any particular form he may need to investigate; but it is only the specialist, who has long worked on the group, who can at once appreciate its dramatic significance. The present reviewer ventures to consider himself an hemipterist of a sort, but his particular speciality has been the tail of the order, as it were, while the first volume of the new catalogue deals with the head. This circumstance furnishes a rather welcome excuse for avoiding all discussion of the numerous disputable points in nomenclature with which the work necessarily bristles, but leaves the way free for remarks of a more general character.

---

[1] "Catalogue of the Hemiptera (Heteroptera)," by G. W. Kirkaldy, Vol. I, Cimicidæ. Berlin, F. L. Dames, 1909.

It is interesting to find that the new catalogue of an order so extensive and of such economic importance as the Hemiptera has been written in the Hawaiian Islands, and published in Berlin. One would have supposed it equally impossible to prepare a work of this sort in such a remote locality, and to persuade a German publisher to bring it out—in English! Here it is, however, and so far as a rather careful scrutiny reveals, it is well above the average of such things in completeness, accuracy and typographical excellence. The price also is reasonable enough. It is no mere list of names and references; localities, food-plants and natural enemies are fully cited, while great care is taken to include all sorts of biological and even embryological citations. At the beginning of each subfamily or tribe is a table showing the geographical distribution of the genera, bringing out various interesting facts. Thus the great number of genera of Acanthosomini in Australia and in the Chilean region is remarkable, and might be offered as an additional argument for a former land connection. It appears, however (if the genera are arranged in correct systematic order), that the Australian and Chilean types stand far apart and are more related to those of the Oriental and Palæarctic regions than to one another. All fossil species are included: the author remarking that "considerable misapprehension regarding these is due to the absurd and unphilosophical separation, by most geologists, of present (*Pleistocene*) time from the rest of the Tertiary (or Kainozoic) as a "Quaternary" epoch. The feeling that the species of the older Tertiary periods are the direct precursors, with but little separation in (geologic) time, of present-day forms, is thus lost, and these interesting relics are regarded with indifference by the majority of entomologists." While it is not probable that the present geological classification will be abandoned, it must certainly be admitted that if the Tertiary period is made to include an amount of time at all comparable to that of its predecessors, we are not merely in the Tertiary at this moment, but not far from the beginning of it!

T. D. A. COCKERELL.

BOOKS

WILLIAM J. GERHARD,
2209 CALLOWHILL STREET, PHILADELPHIA, PA.,

offers the following at affixed net prices. Extended catalogues of books and pamphlets in all branches of natural history post-free on request :

1.	American Journal of Conchology. 7 vols., partly bound	$25.00
2.	American Journal of Science. Second Series, volumes 1–10. Half roan (3 vols. somewhat waterstained)	10.00
3.	American Mineralogical Journal (Bruce). 1 vol., 1814. New half morocco	10.00
4.	American Monthly Microscopical Journal, vols. 1–20 (1888–1899), of which 14 vols. are half roan	15.00
5.	American Naturalist, vols. 1–6 (1868–72)	9.00
6.	Annals N. Y. Academy of Science, vols. 4–14 (1887–1898). Cloth	22.50
7.	Annuaire du Musée Zoologique de l' Académie des Sciences, St. Petersbourg, vols. 1–7 (1896–1902), lacking one number of vol. 1	10.00
8.	Bulletin American Museum of Natural History, vols. 1–11 (1887–1901)	27.50
9.	De Kay. Zoology of New York—Birds. 4to. Cloth. 141 colored plates	10.00
10.	Gaudry, A. Animaux fossiles et géologie de l'Attique. 2 vols., folio, 1862–67. Half calf, 75 plates and map	35.00
11.	Harlan, R. Medical and physical researches, etc. 1835. Cloth	7.50
12.	Journal and Proceedings Royal Society of New South Wales, vols. 11 (1877) to 23 (1890), except vol. 14. Partly bound in cloth	13.00
13.	King, C. United States Geological Exploration of 40th Parallel. Complete set, 7 vols., quarto, cloth, and two folio atlases	22.50
14.	Microscope (The), vols. 4–11. 8 vols. in four. Half roan	7.50
15.	Morton, S. G. Synopsis of the organic remains of the cretaceous group of the United States. 1834. Half roan. Rare	15.00
16.	Pritchard, A. History of Infusoria, including Désmidiaceae and Diatomaceae. Fourth (last) edition. 1861. Half morocco	8.00
17.	Proceedings Lit. and Philos. Society of Liverpool, vols. 1–34 (except vols. 5, 10, 11, 12, 16, 17, 20, 21), partly bound	16.00
18.	Reports of Explorations and Surveys . . . for a railroad from Miss. River to Pacific Ocean. 13 vols. 4to. Bound	12.00
19.	Smithsonian Miscellaneous Collections, vols. 1–6 (1861–67). Scarce	13.50
20.	Sowerly and Lear. Tortoises, terrapins and turtles drawn from life. Small folio, 1872. Half morocco, 60 finely colored plates	11.00
21.	Transactions American Entomological Society, vols. 1–6. Bound. Scarce	35.00
22.	Transactions Geological Society of Pennsylvania. 1 vol. (1835.) All issued. New half morocco. Rare	15.00
23.	Winter, G. Die Pilze Deutschlands, etc., vols. 1 and 2 (1884–87). Half morocco	7.50

Methods in Plant Histology

By CHARLES J. CHAMBERLAIN,

Second edition, revised and much enlarged ; 272 pages, with 88 illustrations, 8vo, cloth ; net $2.25, postpaid $2.39

THE first complete manual to be published on the subject of botanical microtechnique. It contains detailed directions for collecting and preparing plant material for microscopic investigation, setting forth the advantages and disadvantages of the different methods.

Will no doubt find a place in every well-regulated library, and will be found very useful by private students.—*Plant World.*

It is an excellent book for the individual worker and for classes in colleges.—*Education.*

A Laboratory Guide in Bacteriology

By PAUL G. HEINEMANN,

158 pages, interleaved, with 37 illustrations, 12mo, cloth ; net $1.50, postpaid $1.61

A CLEAR and concise presentation of bacteriological technique, designed principally as a manual for the medical student, but highly useful also as a reference book for the biological teacher and investigator, as well as for practical workers in the fields of medicine and hygiene.

The instruction given is clear and accurate, and the practical exercises are well selected.—*The Lancet* (London).

A book such as this must facilitate very greatly the practical class work, for which it is most excellently adapted. — *American Journal of Medical Sciences.*

The directions are clear and concise, and every stage is described so carefully that it is hard to see how the student can go astray. Physicians who are rusty in bacteriology cannot do better than buy this little book. The book is beautifully printed and bound.—*American Journal of Clinical Medicine.*

Animal Micrology:

Practical Exercises in Microscopical Methods

By MICHAEL F. GUYER,

250 pages, 8vo, cloth ; net $1.75, postpaid $1.88

THE title of this book will explain its scope. It is intended as a laboratory manual for textbook use. Its aim is to introduce the student to the technique of microscopic anatomy and embryology, emphasizing details of procedure rather than descriptions of reagents or apparatus. Sufficient account of the theoretical side of microscopy is given to enable the student to get satisfactory results from his microscope.

The directions are simple, explicit, and complete.—*American Journal of Clinical Medicine.*

The medical student will find it very useful as a guide to microscopic work.—*Journal of the American Medical Association.*

This is one of the cleanest works on microscopical technique we have ever seen, and is especially suitable for the beginner. It is full of points, tricks of technique not mentioned in other works, and is one that every student and physician should have.—*Medical Century.*

This valuable book is strong through its rigid exclusion of the trite and the conflicting. It is lucid and helpful, because a man long practiced in practical work has given what he believes the most expeditious and reliable method of obtaining a definite and comprehensive result. — *Medical Notes and Queries.*

A concise, eminently practical, and well-classified treatment.—*Science.*

The expositions of the methods recommended are admirably clear.—*Nature.*

One of the best and most practical works upon microscopic technique with which we are acquainted.—*American Naturalist.*

As a textbook it can hardly be improved. The research worker will find in this book just the information he frequently needs in preparing material with which he is not familiar.—*School Review.*

It does present in very clear form a judicious selection of methods, including an excellent untechnical account of the microscope and its optical principles, adequate for the undergraduate course in histology.— *Journal of Comparative Neurology and Psychology.*

ADDRESS DEPT. 64

Chicago THE UNIVERSITY OF CHICAGO PRESS New York

VOL. XLIV, NO. 520 APRIL, 1910

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page
I. The Origin of the Electricity Tissues in Fishes. Professor ULRIC DAHLGREN 193
II. The Material Basis of Mendelian Phenomena. Dr. REGINALD R. GATES 203
III. Mendelian Phenomena without de Vriesian Theory. Dr. W. J. SPILLMAN 214
IV. The Evolution of New Forms in Viola through Hybridism. Professor EZRA BRAINERD 229
V. Tertiary Archhelenis. Dr. A. E. ORTMANN 237
VI. Shorter Articles and Discussion:
The Probable Origin of the Crinoidal Nervous System: AUSTIN H. CLARK 243
VI. Notes and Literature:
The Question of Sex Determination: Professor H. E. JORDAN. Recent Investigations on the Comparative Anatomy of Conifers: Professor E. C. JEFFREY 245

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

TO ORNITHOLOGISTS AND MUSEUMS

W. F. H. ROSENBERG

Importer of Exotic Zoological Specimens

57 Haverstock Hill, N.W., England

Begs to announce the publication of a new Price List (No. 11) of **Bird Skins**. This catalogue contains over 5,000 species, and is the largest and most complete price list of birds ever published. It is arranged in systematic order, based on the classification of the British Museum "Catalogue of Birds," with authors' names, indications of localities, and an index to families. It will be sent gratis and post free on application, as will the following lists: No. 7, Mammals; No. 8, Birds' Eggs; No. 9, Reptiles, Amphibia, and Fishes.

Largest stock in the world of specimens in all branches of Zoology.

Specimens sent on approval.

Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

Henry Holt & Company

34 West 33d St., New York

378 Wabash Ave., Chicago

Microscopes and Accessories

Hand Cameras of Highest Quality

Binoculars, Prism and Galilean

the best obtainable for Nature Study

Scientific Instruments

Laboratory Apparatus

Max Meyer 18 West 27th St. New York

"Quality, Prices, Service Right."

THE
AMERICAN NATURALIST

Vol. XLIV *April, 1910* No. 520

THE ORIGIN OF THE ELECTRICITY TISSUES IN FISHES[1]

PROFESSOR ULRIC DAHLGREN

PRINCETON UNIVERSITY

Among the many specializations of animal tissues four are so fundamental in nature and so specific in their function that they stand out as exceptionally favorable objects for study, particularly as to their origin and evolution. These tissues are those which produce motion, heat, light and electricity in quantities, and for the benefit of the entire organism.

Of these, motion is the most important. Without the power to move it is probable that few animals would be able to survive and to evolve to any great degree of specialization. Thus the forms which did not develop organs of motion at an early period or those which lost it subsequently would be eliminated and would leave all other and higher degrees of specialization to be attained by such animals as had developed or retained muscle tissue.

Heat production was probably an important factor in the development of many land forms, especially in regions of the earth that became subject to cold, and the possession of any small part of this power would tell to a marked degree in the favorable selection of its possessor.

---

[1] Lecture delivered before the Society of American Naturalists in Boston on December 29, 1909. A fuller technical account with illustrations of the histogenesis of the electric tissue in *Gymnarchus* will shortly appear in another journal.

Of the other two abilities, that to produce light and to generate electricity, we find that both are rare. Luminosity is found to be widely distributed among the various kinds of animals, most of the principal groups having one or more representatives which can produce light. And yet this is, after all, a rare specialization and the percentage of animals which are luminous is very small indeed. It is not so absolutely necessary as the power to move nor can it be regarded as having the selective value that the possession of heat-producing tissues must have. Its real function, sexual, warning, or for purposes of seeing objects in the dark, has not been satisfactorily determined for any groups except possibly the deep-sea fishes and even here we find more to be without it than with it.

As to the last of the dynamic tissues, that which produces electricity, we have here a tissue which is remarkable to an extreme degree both for the rarity of its occurrence and its narrow distribution, is being confined to one group of vertebrates, the fishes, and found here among only seven families.

In these seven groups the tissue seems to have developed absolutely independently and to have formed seven separate types of organ differing markedly from one another in details of structure and position of the organ and yet all adapted, through certain analogous developments, to perform the same function.

We evidently have here a tissue of comparatively recent origin, phylogenetically, and one of the first studies to be made toward a knowledge of its evolution is to find out what can be learned from its history in the individual or its histogenesis.

Of the seven types of organs two are found in elasmobranchs and the remaining five in teleost fishes. The histogenesis of the two elasmobranch forms has been worked out by Ewart, Engelmann, Babuchin, Ogneff and others, but the corresponding history of this tissue in the teleosts has remained unproved with the exception of one form, *Gymnarchus*, the ontogenetic origin of whose electric organ the writer presents below.

Before explaining the histogenesis of the electric tissue in this teleost fish a brief résumé of what is known of the development of the two elasmobranch types of electric tissue should be given.

In the young embryos of *Raja*, Ewart and Engelmann found that the position of the future electric organ was occupied by well-developed muscle in no way different from the other muscle tissue of the trunk. In the half-developed fish the transformation of certain of these single muscle fibers into single electroplaxes was observed to begin, at a later period in those skates which had the simpler types of tissue, at an earlier time in those which had the more highly developed types. This change in the muscle fiber consisted of a widening of its anterior end, which finally resulted in the formation of a flat plate lying at right angles to the position of the former muscle fiber. The posterior end of the fiber degenerated, forming in some cases a useless tail-like appendage in other cases atrophying altogether.

During this change the myo-fibril bundles assumed various curved positions and formed the thick " striated " layer of the electroplax, while the larger part of the cytoplasm formed a flat anterior layer or "electric layer" as well as a thick covering, the nutritive layer, on the posterior surface. This posterior layer was produced into more or less developed papillæ. The nuclei multiplied by amitotic division and were segregated into the anterior and posterior layers, those in the anterior or electric layer forming a very regular layer themselves. The nerve supply, consisting of several medullated fibers, approached the anterior or electric surface and, dividing into very many fine naked branches, terminated in as many disc-shaped plates in this surface.

In the torpedoes, or electric rays, Ogneff has worked out the histogenesis and found that, as in the other elasmobranch forms (the skates), each electroplax develops from one muscle cell. But there are several important differences. The adult organ is a far more highly specialized structure in *Torpedo* than in *Raja* and the muscle cell is still in a very young stage, a mere myo-blast possessing but one nucleus, at the time it begins to change. It is the end furthest from the electric surface or negative pole of the future electroplax that begins to enlarge first into a club-shaped form and then into a disc which continues to expand laterally and grow thinner until it becomes an exceedingly thin plate. The nucleus of the young myoblast or electroblast divides by amitosis into many nuclei, which are distributed through the plate and the nerve supply is large and ends in tiny discs that cover the whole upper, negative or "electric" surface.

In *Gymnarchus,* the only teleost whose histogenesis is known, the electroplaxes of the adult fish are arranged in eight long cylindrical masses, four on each side, and embedded in the muscle of the tail. Each cylinder consists of a row of the thick electroplaxes spaced apart by about their own length of the jelly-like "electric connective tissue" usually found in these organs. Each electroplax conforms to the outline of the cylinder laterally and is bounded anteriorly and posteriorly by surfaces from which a few short blunt papillæ emerge. The electroplax consists of a central core of a fibrillar nature, the fibrils being arranged in the form of approximate layers and giving the appearance of a transverse striation of this region. As will be seen below, this striation does not represent the striation of the voluntary muscle of vertebrates.

This core is covered by a layer of undifferentiated cytoplasm of moderate thickness which contains the numerous nuclei of the syncytium. The nuclei are arranged in a single layer, but, since the central core does not extend into the majority of the papillæ, the nuclei form a central mass in these appendages.

The nerve supply consists of several large medullated fibers which approach each electroplax from the rear and are easily seen to end on its posterior surface. Each of the naked ultimate branches terminates in a knobbed end plate which is imbedded in the substance of the outer layer both on the papillæ and on the posterior surface itself.

The whole cylinder, both electroplaxes and electric connective tissue, is separated from the surrounding muscle tissue by a connective tissue sheath in which a few isolated pigment cells are to be seen. The electroplaxes do not exactly correspond in the adult either to the myotomes or to the vertebræ.

The significant development of the electric tissue takes place between the ninth day of embryonic life, at which time the embryo contains unchanged muscle tissue in its tail, and the 40-day embryo which possesses the organs in practically its adult condition. The critical changes take place within even closer limits; from the 11th day to the 15th would include them. The stages used in this examination were but four in number, the ninth, eleventh, twelfth and fortieth, four out of the seven valuable embryos given the writer by Dr. Arthur Shipley, Dr. Richard Assheton and Dr. J. Graham Kerr, to whom many thanks are due. This material was collected by Mr. John Samuel Budgett in Africa, he most unfortunately losing his life from fever shortly afterwards.

The ninth-day embryo shows no trace of any electric tissue. The myotomes, as shown in a longitudinal section are very regularly formed and are composed at this time of many perfect muscle fibers with the myofibrils developed in several bundles in the peripheral cytoplasm. These muscle fibers are all parallel with one another and with the long axis of the body. Connective tissue is but little developed although it is found sparingly between the muscle fibers.

In the embryo of eleven days the electric tissue has begun to form. Eight regions in each muscle segment, each region composed of a few (10–40) of the young muscle fibers, have become prominent through the slightly greater density of their cytoplasm and the beginning degeneration of the muscle cells which immediately surround them. These eight regions in each myotome lie directly in front of and behind eight corresponding regions in the myotomes before and to the rear of them. They thus mark out anterio-posterior lines which represent the location of the future cylinders. The young muscle fibers composing them retain their myofibril bundles unchanged and the striation of these fibrils is exactly like that of all the other myofibrils in other muscle fibers. The multiplication of nuclei goes on by amitosis as in the regular muscle cells.

The next stages examined are seen in an embryo whose age was between twelve and fourteen days. The word "stages" is used because in such an embryo quite a range of developmental steps can be found, owing to the fact that the tail is still extending and consequently the anterior electroplaxes are older than the posterior. This condition is reversed in the adult, for here it can be seen that the posterior electroplaxes advance further in size and degree of specialization than the anterior ones did. A young stage in this embryo shows that the groups of cells in each myotome which are forming the electroplaxes have become so closely approximated that they form a larger syncytium composed of the several smaller syncytia or muscle fibers which went to form it. This mass has assumed a rather distinct, elongate, spindle-shaped form and each one has increased in length so as to overlap its neighbor both ahead and behind it by a third or more of its length. The myofibrils show a tendency to occupy the central core of the young electroplax and are still striated. In this stage the nerve supply can be seen approaching the spindle from somewhat behind its middle and coming in contact with it at about the junction of its middle and posterior thirds.

The older electroplaxes in this same stage show a change. This change consists in a segregation of the myofibrils in the central core of the mass, where they still run parallel with each other and in a straight anterior-posterior direction; except in the now swollen middle third of the structure where they have assumed a wave-like direction. Furthermore, they have lost the larger part of their striation, this feature being retained only in either end of the fibrils. The less differentiated cytoplasm has become segregated into a peripheral layer and, owing to the more rapid growth in length of the entire body than of the individual electroplaxes, these latter have become drawn apart and no longer overlap as they did at an earlier date.

Before proceeding further a word is necessary as to the fate of the surrounding muscle fibers and the way in which the electroplaxes become marked off from the surrounding tissues.

At first the muscle cells that will be transformed into electric tissue are in direct contact with the surrounding muscle cells of the myotome. Then these immediately surrounding fibers begin to degenerate by a peculiar process of hystolysis that strangely enough resembles somewhat the formation of an electroplax. The middle of the fiber swells up and the myofibrils lose their striation; lastly the ends are drawn in, the nuclei fragment and the whole mass becomes a lump of amorphous matter that finally disappears.

The next developmental changes in the electroplax can perhaps be best described by comparing the stage last described with the practically adult electroplax. In this we find that the middle third of the young form has expanded into the cylindrical body of the completed stage. The two end portions have failed to grow in size and have become one of the several blunt papillæ that have evaginated from both ends. This comparative atrophy of the posterior end of the spindle has left the nerve ending on the posterior surface of the electroplax and on the evagination that project from it, while the anterior end is in contact with a considerable development of capillary blood channels that lie in the electric connective tissue.

Most interesting in this older stage is the fate of the myofibrils. They have lost their striation completely, the dark staining anisotropic substance seeming to have dissolved and left well-defined fibrils of the isotropic substance alone. These fibrils no longer lie so evenly together although still associated in groups. The wave-like direction that they had previously assumed has increased until they now run back and forth at right angles to the axis of the electroplax and consequently in the same relation to their former course. This gives the striated appearance which might be taken for the degenerated remains of the real muscle striation that the developing electroplax formerly possessed.

We thus can see that, while the electroplax of *Raja* and of *Torpedo* were formed from single muscle cells, in the first case by a widening of the negative or electric end and in the second instance by a widening of the positive or nutritive end, the electroplax of *Gymnarchus* is formed by the association of several myoblasts into a single syncytium and the widening of the middle part of this structure into the electroplax.

The other anatomical features of *Gymnarchus* which have caused it to be classed with the *Mormyridæ* demand that a comparison of this organ be made with the apparently widely different organ found in the various mormyrus groups. That found in *Mormyrus Oxyrynchus* will serve as a type and its general plan has been well shown by Ogneff and Schlichter. Here it is evident that a number of consecutive and entire myotomes have been converted into electroplaxes and that the middle layer of each electroplax is composed of unaltered and clearly striated myofibril bundles. The large number of these fibril bundles and their distribution indicate that the whole electroplax is a syncytium composed of all or most of the cells which would otherwise have gone to make up the single myotome. In this we find an agreement with the electroplax of *Gymnarchus* which is also formed from several cells. In the one case all the cells in the myotome have been used; in the latter only those lying in eight particular localities.

Further homology is seen in the disposition of the probably superfluous myofibrils. In both forms they are relegated to a middle position in the electroplax while the apparently more important cytoplasm forms layers on the anterior and posterior surfaces of the structure. Also, in both, the now useless myofibril bundles are packed out of the way at right angles to the axis of the electroplax which remains the same as the former axis of the muscle cells that were used to form it.

The only difference lies in the fact that the striation of the fibrils is retained in the *Mormyrus* forms while it is lost in *Gymnarchus,* the dark-staining anisotropic substance apparently dissolving away.

From what little can be predicted concerning the possible origin of the electric tissue in the other teleost forms it is probable that the Mormyridæ (including *Gymnarchus*) are the only fish in which the electroplax is formed as a syncytium from more than one cell. In *Astroscopus, Electrophorus* (forming *Gymnotus*) and *Malopterurus* the structures show every evidence of having been developed from single myoblasts with the exception of *Malopterurus,* where it is a question as to whether they are not evolved from gland cells instead.

The evolution of these structures was most probably not based upon a natural selective basis. It is true that all muscle cells produce a slight static discharge at the moment of contraction, and that the far greater shock given by the electroplax is possibly a development of this same discharge. But Darwin in his "Origin of Species" has already said that the electric organs of fishes were one of the serious obstacles in the way of his natural selection theory, showing that the very slight discharge of the more primitive organs could not possibly have been useful to their possessors to the extent of an excluding selection based on their presence or degree of development.

Some good evidence as to the methods of evolution ought to be deduced from the degree of specialization and distribution of electric organs in some of the groups; even if experimental work seems at present to be impossible. In the skates, for instance, we find a very even and general distribution of an organ and tissue that is apparently in course of evolution, but which has not yet arrived at a state of efficiency. It seems that the organ must have originated in the common ancestor of the thirty or more species of skates found in the seas of the world.

All the Rajidæ have this organ and yet their close allies show no sign of its appearance. One form in particular was formerly classed with the skates, but some years ago was removed on anatomical evidences from this group by D. S. Jordon and classed in another genus. The writer dissected a specimen of this species with great interest and care and found that there was no trace of electric tissue. And yet this species is undoubtedly closely related to the skates and must have inherited at least their potential powers to develop electric tissue. Furthermore this species is skate-like to an extreme degree in form and habit and must have lived under conditions and surroundings similar to those which we must assume were the ones, if any, that stimulated the skate ancestors to change muscle tissue into electric tissue. Evidently there are internal as well as external conditions and stimulæ to be taken into account.

Likewise among the torpedoes; all possess a very highly developed organ, evidently a common inheritance from some ancestor in which it originated. Subsequent variation in the tissue has not kept pace with the fair amount of external variation in the several species. It seems that the impulse to evolve this tissue has extended into all the members of these two groups, a real inner stimulus working independently of outer condition.

On the other hand, other groups of similar form, appearance and mode of life to some of the other electric fishes absolutely lack the electric tissues. These may or may not be nearly related. A rather remarkable example is to be seen in *Astroscopus* and its related form *Uranascopus scaber*. These two fish look so much alike that one may be used to show the fishermen what the other looks like. Their habits are practically the same. Also this feature is noticeable among the Gymnotidæ, whose various members show many grades of specialization but have not been sufficiently studied as to the possession of rudimentary electric organs. These studies together with the histogenesis of other teleost electric tissues, particularly that of *Malopterurus*, are most attractive fields for future work.

THE MATERIAL BASIS OF MENDELIAN PHENOMENA [1]

DR. REGINALD R. GATES

Missouri Botanical Gardens, St. Louis, Mo.

Since the rediscovery of Mendel's results at the beginning of the century, a very extensive and important field of hereditary phenomena has been actively developed, and the conceptions and explanations of Mendelian behavior have been changing with great rapidity. Many explanations and views of the phenomena of dominance, recessivity, latency and segregation have been proposed, and the only conception of Mendel which has remained essentially unmodified by Mendelians is that of the purity or unity of the characters in the gametes. Even this conception has been viewed by various workers in many lights, with a more or less complete and sweeping denial of an actual segregation of characters in the germ cells.

In the time at my disposal I shall bring before you the results of only one *Œnothera* cross, which shows Mendelian behavior in certain characters, and in the discussion of these results shall point out certain modifications of our conceptions of Mendelian segregation which they necessitate.

The cross in question is *Œnothera nanella* × *O. biennis*, *O. nanella* being a mutant from *O. Lamarckiana* and the *O. biennis* in the cross being from a wild race growing around the New York Botanical Garden. The seeds were first obtained from Dr. D. T. MacDougal. In the F_1 of this cross two types were produced, evidently corresponding to DeVries's twin hybrids. One of these types breeds true in the second generation and is the same as the type obtained in the F_1 of *O. Lamarckiana* × *O. biennis*. The other is a new type, with unexpected characters, which I have called *O. rubricalyx.* None of the peculiar characters of either parent are present in this hybrid. But this is not so remarkable, because crosses between the *Œnothera* mutants frequently lose the distinctive marks of both parents and give *O. Lamarckiana.* The same form, *O. rubricalyx*, has appeared in my cultures as a mutant or extreme variant from *O. rubrinervis,* from which it differs only in possessing a red hypanthium instead of green, a marked increase in the red color pattern of the sepals (the median ridge of the sepals being also red instead of green), and in the production of a conspicuous quantity of red pigment on the *under* surface of the petioles of the rosette leaves, as well as in other parts of the plant. The type can therefore easily be recognized by observing the under surface of the rosettes, and in the flowering stage the conspicuous deep red buds render the plant very attractive and showy, distinguishable from *O. rubrinervis* at a glance. It differs from *O. rubrinervis* in its greatly increased capacity for anthocyanin production, a difference which expresses itself in nearly every organ of the plant. A full illustrated account of this cross will be published elsewhere.

---

[1] This paper was presented before the American Society of Naturalists in Boston, Mass., December 29, 1909.

In the F_2 this type splits in the Mendelian ratio of 3:1, giving approximately 75 per cent. *O. rubricalyx* and 25 per cent. *O. rubrinervis.* I have not yet bred the later generations, but the *O. rubrinervis* may be expected to breed true and the *O. rubricalyx* to split as before.

In this single cross there are many facts which throw interesting side lights on the nature of Mendelian behavior. In the first place, only one character splits in Mendelian fashion, the others remaining true. Hence, if proof of this proposition were needed, here we have proof that Mendelian phenomena are not universal, even in the forms in which they occur. The *O. rubricalyx* which appeared as a mutant from *O. rubrinervis* also splits in the same manner, a certain number of the offspring reverting to the *rubrinervis* condition, though I have not been able to determine whether this is a Mendelian ratio. These and other facts make it very probable that the explanation of Mendelian phenomena is to be sought in the nature of the character itself, which conditions and perhaps determines this type of inheritance.

Another important point in connection with this hybrid is that the split in the F_2 does not produce a return to the condition of one of the grandparents, as in typical Mendelian behavior, but the difference between the two types of the F_2—*O. rubricalyx* and *O. rubrinervis*—is a purely quantitative difference, in capacity for pigment production, although morphologically this difference is expressed in certain very definite regions of the plant. There are no intermediates between these two types, each being an independent condition of stability. The difference, therefore, clearly dates back to the germ cells.

That a quantitative difference between germ cells in their capacity for pigment production can behave in Mendelian fashion, showing the phenomena of dominance and segregation, is of fundamental significance in the interpretation of the nature and material basis of these phenomena.

Riddle ('09) has brought together in an interesting way the facts of physiology and biochemistry which show that the various pigment colors in mammals and other animals are different stages in the oxidation of a single melanin pigment by the enzyme tyrosinase. In the light of the facts of quantitative Mendelian inheritance which I have presented, it is clear that color inheritance in the mammals can also be most easily interpreted as a case of quantitative inheritance, due to initial quantitative differences of some sort in the germ cells themselves. It is not impossible that nearly all Mendelian inheritance may be found, on sufficient analysis of the characters, to be of this sort. Studies in variation show that many apparently qualitative differences, when analyzed, are found to be purely quantitative in origin. It should be remembered in the case of melanin pigments, as Riddle also points out, that while some tyrosin oxidations lead to the formation of melanins, others result in the usual waste products, such as carbon dioxide and ammonia. Of course, only the former can be of significance in inheritance, and it is probable that whatever determines in how far the former process of tyrosin oxidation shall take place, will be found to control or determine these quantitative differences in the end-products of the germ cells.

It is interesting and suggestive to note in this connection that Morgan ('09) has adopted a quantitative interpretation of the sex-determining factors in the germ cells of insects and other organisms.

It is important to enquire what is the nature and origin of this quantitative difference, such as must occur in the germ cells of the hybrids I have described. It is most reasonable to suppose that it originates at the time the germ cells are formed, *i. e.*, during the reduction divisions, for the whole individual from a very early stage of the seedling to mature development shows one or the other of the alternative characters. Hence, the germinal difference must date back to the fertilized egg, and if this be true we must logically take it back farther still, on account of the definite Mendelian proportions, to the individual germ cells which united in fertilization, and hence probably to the reduction divisions.

The question of the relation of the chromosomes to Mendelian behavior has been so often discussed that I will only touch upon it here, to point out that the theory of qualitative hereditary differences among the chromosomes is not incompatible with the view that differential Mendelian characters are properties of the germ cell as a whole. If, during the reduction division, certain of the chromosomes which are segregated into separate cells are chemically unlike, then different groupings will arise and the whole germ cells whose nuclei the different groups enter will soon experience the effect of those differences, and accordingly such germ cells would be expected to become unlike as a whole. This follows necessarily, not only from the continual active interchanges in metabolism between nucleus and cytoplasm, but from the unity of the cell, which modern biology has abundantly proved. Hence there is no difficulty in supposing that differences which must be thought of as characterizing the germ cell as a whole, originated from chromosomal differences during reduction. On the other hand, there seems no necessity for assuming that *all* germinal differences originate in the chromosomes, although if they originated in the cytoplasm it is necessary to assume as a *vera causa* either a separation of cytoplasmic substances during reduction, of which we have no visible evidence, and which seems unlikely for various reasons, or *quantitative* cytoplasmic differences in the cells of a tetrad. The quantitative difference which must exist between the germ cells of *O. rubricalyx* and *O. rubrinervis* may possibly be conceived of as originating in the cytoplasm and then becoming a property of the germ cell as a whole.

It is even possible that this is not a difference in amount of matter of any sort, but rather in the energy-content of the two types of germ cell, although we have no means of knowing how or why such a marked difference in energy-content should arise.

To attempt to account for the manner of origin of a *O. rubricalyx* mutant from a *O. rubrinervis* germ cell would at the present time be purely speculation. DeVries' conception of a new unit becoming suddenly activated in the germ plasm seems too formal an assumption to be accorded the dignity of an explanation. The fact that the *O. rubricalyx* mutant reverts to *O. rubrinervis* may be looked upon as evidence in favor of his view that a mutant originates as a hybrid, from the union of a mutated with a non-mutated germ cell.

I should also point out that the origin of *O. rubricalyx* from *O. rubrinervis* may perhaps be significant as indicating an orthogenetic tendency to an increase of pigment production, although this increase has taken place by definite germinal steps, particularly in the origin of *O. rubricalyx* from *O. rubrinervis.*

The significance of the fact that I have succeeded in producing *O. rubrinervis* as one of the types resulting from this cross, is too obvious to require pointing out. In the light of these facts, it is not impossible that other mutants can be similarly synthesized.

Much experimental work has been directed to the study of the physiology of anthocyanin production in the plant. Without entering into the details of this work it may be said that two general theories of anthocyanin production have been developed. E. Overton ('99), Mirande ('07), Molliard ('07) and others conclude that it arises from an accumulation of sugars in the cell sap, which unite with tannic acid to produce a glucoside. Overton showed experimentally that low temperature and high light intensity both cause anthocyan production. Mirande ('07) called attention to the development of red in leaves eaten by insects;[2] and Combes ('09*a*) produces the same result by annular decortication. In every case the result is interpreted as due to an accumulation of sugars. J. Laborde ('08), from his experiments deduced a slightly different view, namely that formaldehyde or one of its polymerization products may cause tannin transformation, to produce color. Further, Overton, Laurent, Molliard and others, found that various seed plants grown in sugar solution show a marked increase in anthocyan production, which indicated clearly a relation, direct or indirect, between the presence of sugars and the development of anthocyan. Whether such an increase in anthocyan production is inherited is not known, but presumably it would not be inherited. Of course, many variations in pigment production are of a non-heritable sort, but it is equally certain that in *O. rubri-*

[2] In this connection I may call attention to certain observations of my own upon the effects of the attacks of a certain insect on the buds of *Œnothera*. The very young buds are stung by this insect and such buds undergo several characteristic changes in development. The hypanthium fails to develop and the base of the cone becomes very thick. In *O. Lamarckiana* (and the same is true at least of several mutants) there is also always a conspicuous amount of red developed on the sepals under these circumstances, but the buds of *O. biennis*, while they undergo the same morphological changes, never develop any red.

calyx the increased pigment production is a heritable character, and therefore the change which brought it about must have been of a fundamental sort, in the germ plasm.

A more recently developed hypothesis of anthocyan formation, suggested by Pick in 1883 and supported by the work of Palladin ('08), Buscalioni and Pollacci ('04), in their extensive memoir, and others, is that anthocyan originates from the action of oxydases upon the respiratory chromogens of the cell, the latter being aromatic bodies which on oxidation yield colored compounds. The experiments of Molliard ('09) support the latter theory by showing the necessity for the presence of oxygen in anthocyan production. Molliard also showed that, when grown in a sugar solution, the respiratory exchanges of plants are more intense.

Combes ('09*b*) has recently harmonized the two theories. He shows that there is a close relation between the production of anthocyan and an increase in the proportion of sugars and glucosides in the cell sap. He concludes that since the formation of anthocyan, a compound of glucoside nature, is correlative with an increase of the total glucosides, the anthocyan cannot be formed from preexistent glucosides, but from some other source; and since there is also an increase in chromogens (Palladin) therefore anthocyan is not derived from chromogens already existing, but its formation must be provoked by the accumulation of sugars, which increases the respiratory exchanges and appears to determine the acceleration of oxidation processes. Under these conditions the production of glucosides is increased, and these are, in part at least, anthocyanins.[1]

It is scarcely necessary to point out that, whatever may be the chemistry and physiology of anthocyanin production, in the case of *Œnothera rubricalyx* there must have been a fundamental change in the germ plasm by reason of which, under the same external conditions as *O. rubri-*

---

[1] See also the important recent papers of Miss M. Wheldale. Proc. Roy. Soc. London B, 81: 41–60. Proc. Cambridge Phil. Soc. 15: 137–168 and Reports to the Evolution Committee of the Royal Society, V., pp. 26–31, 1909.

nervis, it reacts with much greater pigment production; a reaction which shows itself with great definiteness in the buds and the rosette leaves.

Although plants and animals equally exhibit Mendelian phenomena, yet the part of the organism which must be looked upon as constituting the germ plasm, and hence the basis of such phenomena, shows several important differences in Metazoa and Metaphyta, two of which may be pointed out. Most important of these differences is probably the absence of a *Keimbahn* in plants, in the sense in which it is known to be present in many animals. The classical cases of *Ascaris* (Boveri) and *Cyclops* (Häcker) need only be cited. More recently, other work, such as that of Hegner ('09) in the Coleoptera, has shown that the germ cells are formed from certain free nuclei, at an early stage in the segmentation of the egg. Thus set aside, they rest and undergo very few divisions, until a late stage of embryonic life. There is no evidence whatever of a similar process in higher plants, and it is probably made impossible by the method of plant growth. On the other hand, it may be pointed out that while, in plants, there are no resting cells set aside in the body tissues, to serve later as reproductive cells, yet a lineage of cells exists, which may be looked upon as a *Keimbahn* in one sense. Every one who has studied plant embryos recognizes their characteristically large nuclei with huge nucleoli having a large chromatin content. A similar appearance is characteristic of all undifferentiated meristematic cells, so that such cells, forming a lineage from the egg cell to the spore mother cells, may be thought of as constituting a *Keimbahn* for the plant, though evidently in a somewhat different sense from that in which the term is employed for animals. The fact that in such a lineage, a great number of cell generations intervene between the fertilized egg and the spore mother cell, together with the fact that the meristematic cells forming this lineage are near the surface of the plant, where they are almost directly exposed to environmental influences (and not hidden away in the interior of the body as in animals), doubtless accounts for the greater plasticity exhibited by plants. Indeed, it is a matter for wonder that, under these conditions, plants show such hereditary constancy. The accurate reproduction, generation after generation, of the most minute hereditary differences, shows the relative fixity of the material of the germ plasm.

The work of the Marchals ('06 and '07) with the mosses seems to show clearly that, during the meiotic divisions of spore formation, an actual segregation of sex-producing tendencies or elements takes place. Much other evidence of a similar sort in plants might be cited if time permitted, and the case of the sex chromosomes in insects is too well known to require more than mention. But while the reduction divisions seem the most natural place to look for an explanation of the Mendelian proportions, yet on the other hand there is much evidence that the phenomena of "splitting" also occur at other times in the life history. Bateson ('05) has shown that in two races of sweet peas (*Lathyrus odoratus*), one of which has long pollen grains and the other round, the long pollen character is dominant in the F_1. If a segregation of characters took place here during the reduction divisions, we should find 50 per cent. of each type of pollen grain. But plants having long pollen give only long, or they may give three plants with long pollen to one with round. Only in "very rare and exceptional" cases is there a mixture of long and round in the same plant, and in such cases they are found only in certain flowers of an individual. Rosenberg ('06) found that in the hybrid *Drosera longifolia* × *D. rotundifolia,* in some cases two pollen grains of a tetrad resemble each parent, the grains differing chiefly in size. More recently, however, he has found ('09) that the variations in the size of the hybrid pollen grains probably depend upon the numbers of chromosomes which enter the respective daughter nuclei during reduction, and hence this difference in pollen grains will no longer serve as evidence for a segregation of characters at this time.

There is nothing to indicate that the phenomena of vegetative splitting, or reversion to the parental types, in such forms as the reputed graft-hybrid, *Cytisus Adami,* differ in any essential respect from Mendelian segregation in germ cells. In angiosperms, the great majority of which are hermaphrodite, there is a separation of tendencies, which may be thought of as a "segregation," in the Anlage of every flower, the stamens producing microspores and male gametophytes, while the ovules bear the megaspores, which develop the female gametophyte. These two tendencies—namely, for the stamens to produce microspores and the ovules to produce the female gametophyte—are almost never interchanged (although Němec, '98, has described a case in *Hyacinthus,* in which the microspores may produce a structure resembling more or less the female gametophyte). Whether there is here a separation of substances in the cytoplasm or chromoplasm during the division of certain cells in the Anlage of the flower, is not known, but it is not impossible that such is the case.

Viewed from this standpoint, all differentiation during ontogeny may be considered a "segregation." A consideration of what this really consists in would involve the whole great problem of individual development, which I shall not touch upon here. But it may be pointed out that maturation, particularly in Mendelian hybrids, may be looked upon as a period of active germ cell differentiation.

The factors involved in such differentiation may be, in some cases, quite as complex as those involved in development itself, but as I have shown from the evidence of these *Œnothera* hybrids, and as appears from color inheritance in mammals and from other evidence, in many cases at least the difference between Mendelian germ cells must be of a simple quantitative sort, involving either a difference in the amount of certain material substances or a difference in the energy-content of certain constituents.

From this point of view, many instances of Mendelian behavior are seen to be cases of quantitative inheritance.

LITERATURE CITED

Bateson, W., Saunders, Miss E. R., Punnett, R. C., and Hurst, C. C. 1905. Report II. to the Evolution Committee of the Royal Society. Experimental studies in the physiology of heredity. London, pp. 154.

Buscalioni, Luigi e Pollacci, Gino. 1904. Le antocianine ed il loro significato biologico nelle piante. *Atti dell' Instituto Bot. univ. di Pavia,* 2d Ser., 8: 135–511, pls. 7–15.

Combes, R. 1909. Production d'anthocyane sans l'influence de la decortication annulaire. *Bull. Soc. Bot. de France,* 56: 227–231.

—— 1909. Rapports entre les composés hydrocarbonés et la formation de l'anthocyane. *Ann. Sci. Nat. Botanique,* 9: 275–303.

Hegner, R. W. 1909. The origin and early history of the germ-cells in some Chrysomelid beetles. *Journ. Morph.,* 20: 231–296, pls. 4.

Laborde, J. 1908. Sur le mechanisme physiologique de la coloration des raisins rouges et de la coloration automnale des feuilles. *Comptes Rendus,* 147: 993–995.

Marchal, Élie and Émile. 1906. Recherches expérimentales sur la sexualité des spores chez les mousses dioïques. *Mém. couronnés, Acad. roy. de Belgique,* 1.

—— 1907. Aposporie et sexualité chez les mousses. *Bull. Acad. roy. de Belgique,* 1907: 765–789.

Mirande, M. 1907. Sur l'origine de l'anthocyanine déduite de l'observation de quelques insectes parasites des feuilles. *Comptes Rendus,* 145: 1300–1302.

Molliard, M. 1907. Action morphogenique de quelques substances organiques sur les végétaux supérieures. *Rev. gén. de Bot.,* 19: 241–291, 329–349, 357–391, pls. 8, 9, 10 and 13, figs. 52.

—— 1909. Production expérimentale de tubercules blancs et de tubercules noir à partir de graines de Radis rose. *Comptes Rendus,* 148: 573–575.

Morgan, T. H. 1909. A biological and cytological study of sex determination in Phylloxerans and Aphids. *Journ. Exptl. Zool.,* 7: 239–352, pl. 1, figs. 23.

Němec, B. 1898. Ueber den Pollen der Petaloiden antheren von Hyacinthus orientalis L. *Bull. Int. Acad. Sci. Bohême,* 5: 17–23, pls. 1–2.

Overton, E. 1899. Beobachtungen und Versuchen über das Auftreten von rothem Zellsaft bei Pflanzen. *Jahrb. Wiss. Bot.,* 33: 171–231.

Palladin, W. 1908. Ueber die Bildung der Atmungschromogene in den Pflanzen. *Ber. Deut. Bot. Gesells.,* 26a: 389–394.

Pick, H. 1883. Ueber die Bedeutung des rothem Farbstoffes bei den Phanerogamen und die Beziehungen desselben zur stärkewanderung. *Bot. Centlbl.,* 16: 281–284, 314–318, 343–347, 375–382, pl. 1.

Riddle, Oscar. 1909. Our knowledge of Melanin color formation and its bearing on the Mendelian description of heredity. *Biol. Bull.,* 16: 316–351.

Rosenberg, O. 1906. Erblichkeitsgesetze und Chromosomen. *Botaniska Studier,* 1906: 237–243, figs. 5.

—— 1909. Cytologische und morphologische Studien über *Drosera longifolia rotundifolia × rotundifolia. Kungl. Svenska Vetenskapsakad. Handl.,* 43: 1–64, pls. 1–4.

MENDELIAN PHENOMENA WITHOUT DE VRIESIAN THEORY[1]

DR. W. J. SPILLMAN

U. S. DEPT. OF AGRICULTURE

THAT the phenomena of Mendelian segregation of character pairs is inextricably linked with the de Vriesian notion of pangenes is an opinion widely held, both by the advocates of the theory of discontinuous variation and by the opponents of that theory. Professor S. J. Holmes was one of the first American biologists to point out the fallacy of this idea.[2] He called attention to the fact that due consideration of the phenomena reported by Mendelian investigators did not lead to the theory of discontinuous variation as a necessary consequence.

While in the present paper it is my purpose to present an explanation of Mendelian phenomena without resorting to the idea of unit characters, I do not wish to be understood as belittling the important work done by de Vries and his followers. While contending that the de Vriesian doctrine that organisms are aggregates of separately heritable characters is unsound, I believe this investigator has uncovered a new type of variation which must be reckoned with as *a* means of evolution, not by any means the sole, or even the most important, means. For want of space, I am compelled, in what follows, to present some opinions without submitting all the evidence in favor of them. However, an attempt will be made later to present this evidence more fully. It seems to the writer that what Darwin considered to be fluctuating variations, amenable to the action of natural selection, may now be regarded as consisting of four distinct types of variation. First, we have those variations in the progeny of a given individual, or pair of individuals, which are due to what we may call "Mendelian recombination of characters."

---

[1] This paper was presented before the American Society of Naturalists, in Boston, Mass., December 29, 1909.

[2] See AMER. NAT., May, 1909.

Natural selection may have a very important influence on variations of this kind, since the variations are hereditary. The recognition of variations of this type must of course be attributed to Mendel, but de Vries, Correns, Von Tschermak and perhaps some others must be recognized as rediscoverers of this principle.

In the second place, after we have eliminated all variation caused by Mendelian recombination we still have a type of variation which is more and more coming to be called fluctuation, and which is due wholly to environment. Such variations are now believed not to be hereditary and therefore not amenable to the action of natural selection. In this connection we need only mention the important investigations of Johanssen on beans and barley,[3] the work of Nilssen and his able staff at Svalöf on wheat, oats and other species, and the recent classic work of Jennings on *Paramecium*.[4] The work of these investigators indicates strongly that selection is without effect on fluctuations due to environment. Dr. E. M. East, in Illinois Experiment Station Bulletin No. 127, reaches the conclusion that no effect of selection has been proven in clonal varieties of potatoes.

In the third place, de Vries found a type of variation which the cytological work of Gates,[5] Rosenberg[6] and Gager,[7] indicates to be due to irregularity in the distribution of chromosomes in mitosis.

Gates has shown that in the species with which de Vries worked there are irregularities in chromosome distribution. Furthermore, de Vries has shown that his mutants differ from each other in almost every detail, just as we should expect them to do if each of the chromosomes is more or less responsible for the whole process of development.

---

[3] W. Johannsen, "Ueber Erblichkeit in Populationen u. Reinen Linien," Jena. Fisher, 1903; Rep. 3d Int. Con. on Genetics, pp. 98–113.

[4] H. S. Jennings, *Proc. Amer. Phil. Soc.*, XLVII, No. 190, 1908; *Jour. Exp. Zool.*, Vol. 594, June, 1908.

[5] R. R. Gates, *Science*, January 31, 1908; *Science*, February 12, 1909, and elsewhere.

[6] O. Rosenberg. Rep. 3d Int. Con. on Genetics, pp. 289–291.

[7] E. Stewart Gager, Publications of New York Botanical Garden.

Rosenberg has shown that the irregularity of certain first-generation *Hieracium* hybrids is accompanied by irregularity in the number of chromosomes present.

Quite recently Gager, in his study of the effect of radium emanations on plants, has not only produced mutants apparently of the character of those found by de Vries, but has shown that in mitosis in treated specimens there is irregularity in the distribution of chromosomes. The writer some time ago suggested a similar explanation for the interesting work of McDougall in which mutants were produced by chemical stimulants. The behavior of the Rubus hybrid produced by Burbank, and resulting in the *Primus* berry, is so closely parallel to that of *Hieracium* hybrids studied by Rosenberg that a similar explanation at once suggests itself.

Boveri's classic work on the relation of chromosomes to development strongly supports the view that the de Vriesian mutants are due to loss or exchange of chromosomes, and this view is consistent with the work of Wilson, Morgan, Stevens and others on the relation of the chromosomes to sex.

I think, therefore, that we are in position to recognize, at least tentatively, a new type of variation, which is due to irregularities in the distribution of chromosomes, and which I shall call "de Vriesian mutation." These variations, being hereditary, are amenable to the action of natural selection, and must therefore be recognized as one method of evolution. In a certain sense these mutations are discontinuous, and the reason for this is apparently clear.

When we consider all the facts in the case, which I have not time here to outline, I think that few biologists will contend that all evolutionary changes are due to Mendelian recombination, or to de Vriesian mutation as defined above. The enormous diversity in groups having the same number of chromosomes, as well as observable differences in the chromosomes themselves, render any such view untenable. I therefore postulate a fourth kind of variation due to fundamental changes in what we may call the germ plasm, and I am inclined to believe that this is by far the most important type of evolutionary change. Whether changes of this character are continuous or discontinuous is not a very important question. It is more important to ascertain their cause and nature. I imagine they are largely chemical changes in the composition of, or changes in the relative amounts of substances present in, the germ plasm. If these changes are continuous the work of Johannsen, Nilssen, Jennings and East, above referred to, indicates that they are very slow. Such changes are certainly hereditary, and are thus a factor, and I believe the most important factor, in evolution.

One point regarding fundamental changes in the germ plasm it is important to remember: a gradual change might go on for a long time in the chemical activity of the cell before reaching a point where any outward manifestation of this change would appear. For instance; in some purple flowers there is reason to believe that the color is due to some such action as that of acids and alkalies upon the color of litmus, the flower being red or purple according to the amount of some substance present. Now a gradual change might go on in the relations between the substances concerned without producing any visible effect until a certain point is reached, when a marked effect is produced, giving what appears to be a discontinuous change, but what may be in reality a critical point in a slow and gradual change.

Riddle, in his recent very interesting paper on melanin color formation[8] has shown that in all probability melanin colors develop as the result of the action of an enzyme upon a chromogen, and that this action is a complex one. The chromogen is first converted into a new substance, the same enzyme then converts this substance into a third, and so on, producing a long series of substances. The early numbers in this series give no color, but finally a stage is reached where a number of steps in the series give color. Riddle seems to think that all the melanin colors found in organisms should be referred simply to the different stages of a single process of oxidation. This, however, can hardly be true. The fact that we get two or three kinds of pigment deposited in the same region of the organism, apparently at the same time, would indicate that there is more than one oxidation process involved. Furthermore, Riddle himself points out that, while in some oxidation processes series of colors occur extending from light yellow to black, with reds and browns as intermediates, in others the final stages of the oxidation processes are red. Quite a number of different oxidation processes are cited. Now the facts of color inheritance indicate that there may be several oxidation processes, and that in some of them a given color, for instance, red, appears as soon as color appears at all.

---

[8] *Biological Bulletin*, May 1909, pp. 316–351.

Assuming that the production of enzyme and chromogen is a general function of protoplasm, and assuming further that the relative amount of enzyme and chromogen present have a determining influence on the stage which the oxidizing process reaches in the organism, the phenomena of Mendelian color inheritance are easily explained without recourse to the idea of unit characters at all, as I shall now attempt to show. It must be understood that the figures in the following tables are merely illustrative and are not meant at all to indicate actual amounts.

TABLE I

Red and White Peas

Organs.	Relative Contributions.		F_1	F_2		
	Pure Red.	Pure White.		*BB*	*BB'*	*B'B'*
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
Cy	25	25	25	25	25	25
AA	15	15	15	15	15	15
BB	30	10	20	30	20	10
CC	8	8	8	8	8	8
DD etc.	22	22	22	22	22	22
	100	80	90	100	90	80
	Red	White	Red	Red		White

Let us consider first the cross between red and white sweet peas, in which generation F_1 of the hybrid is red and generation F_2 gives us the ordinary Mendelian ratio of three red to one white. Table I shows an explanation of the Mendelian results on the assumption that every organ in the cell is concerned in color development. It is assumed in this instance, merely for purpose of illustration, that when the amount of enzyme present in the cell is 85 per cent. or more of the amount found in pure red races the oxidation process reaches the stage necessary to produce red coloration. The same end results would occur if, because of some peculiarity of a *single pair* of chromosomes in the white race, as compared with the red, the end result of the oxidation process in the white race gives no color.

In the first column of this table *Cy* represents the cytoplasm, and, in fact, all of the organs in the cell except the paired chromosomes. *AA, BB,* etc., represent pairs of homologous chromosomes. The second column gives assumed relations between the amount, say, of the enzyme produced by the different organs of the cell in the pure red race. It is assumed, for instance, that all the organs of the cell except the chromosomes produce 25 per cent. of this enzyme. The first pair of chromosomes produce 15 per cent., the second pair 30 per cent., and so on.

Now, with the assumptions made, a white race would result if a single pair of chromosomes produce markedly less of the enzyme than they produce in the red race. Column 3 shows the hypothetical conditions in such a white race. In the table it is assumed that in the red race the second pair of chromosomes produce 30 per cent. of the total amount of enzyme present, while in the white race, for some reason, this pair of chromosomes produces only one third of the enzyme it does in the red. Thus, in the white race we have only 80 per cent. of the amount of enzyme present in the red, and not enough to carry the oxidation process to the point of giving red coloration. The hybrid between these two races will have one chromosome producing its 15 parts and another chromosome producing only 5 parts, thus giving 20 parts where in the red race we had 30. In all, there is in the hybrid 90 per cent. as much of the enzyme as in the pure red. With the assumptions made the hybrid would therefore be red.

It is well known that heterozygotes frequently present vegetative vigor much greater than that of the related homozygotes. This may be possibly due to the greater opportunity certain chromosomes have of making more growth before filling the cell with their products. If such is the case, then the enzyme produced in our hybrid might exceed the mean between that produced in the two races crossed. This would explain the preponderance of cases in which the heterozygote resembles that parent which represents the more advanced ontogenetic stage. But there are not a few cases in which the heterozygote resembles the other parent. This happens to be the case in two of the first cases of dominance made out by the writer; namely, beards in wheat and horns in cattle. Both of these characters are recessive; or, as the de Vriesians would say, in them, absence is dominant to presence. Under the present hypothesis, we do away entirely with the presence and absence hypothesis, as will be seen later.[9]

In generation F_2 (Table I) one fourth of the progeny would possess a pair of chromosomes each of which produces its 15 parts of enzyme. One half of the individuals would have one chromosome producing 15 parts and another producing 5, while the remaining fourth of the individuals would have a pair of chromosomes each of which produces only 5 parts. We thus have one fourth of the population producing the normal amount of enzyme, half of it producing 90 per cent. of this, and one fourth of it producing only 80 per cent. This would give us three red individuals to one white.

It must be remembered that I am merely attempting to show here that it is possible to make assumptions that will explain Mendelian phenomena without resort to the idea of unit characters.

In Table II we have a more complex case; namely, that of the cross between red and white *Antirrhinums* reported by de Vries. In this cross de Vries found what is ordinarily called two pairs of Mendelian characters. Under the assumptions I have made this simply means that in the white race there are two pairs of chromosomes which were deficient in the amount of enzyme produced as compared with the pure red race used by de Vries in this cross.

---

[9] See article by Shull in AMERICAN NATURALIST, July, 1909.

TABLE II

RED AND WHITE ANTIRRHINUMS

Organs.	RELATIVE CONTRIBUTIONS.		F_1	F_2								
	Pure Red.	Pure White.		$AACC$	$AACC'$	$AAC'C'$	$AA'CC$	$AA'CC'$	$AA'C'C'$	$A'A'CC$	$A'A'CC'$	$A'A'C'C'$
	%	%	%	%	%	%	%	%	%	%	%	%
Cy	24	24	24	24	24	24	24	24	24	24	24	24
AA	30	*14*	22	30	30	30	22	22	22	14	14	14
BB	12	12	12	12	12	12	12	12	12	12	12	12
CC	26	*22*	24	26	24	22	26	24	22	26	24	22
DD etc.	8	8	8	8	8	8	8	8	8	8	8	8
	100	80	90	100	98	96	92	90	88	84	82	80
	Red	White	R	Red						Del.		Wh.

In the third column of Table II we have 14 parts of enzyme instead of 30 in the second column (chromosomes *AA*), and 22 parts instead of 26 in the second column (chromosomes *CC*). Since the hybrid gets one of each pair of chromosome from each of the parents it has 22 parts instead of 30, and 24 instead of 26. If, in this case, the amount of enzyme present in the cell is 85 per cent., or more of that present in the original red race with which de Vries worked, it is assumed that the oxidation process will reach the red stages. The hybrid in this case is red, though perhaps not so deep a shade of red as the pure red race.

In generation F_2 of this hybrid we have nine types. The first type is like the pure red race with which de Vries started. The third of these types is another pure race, but with a lessened amount of enzyme, and presumably less intense red color. The seventh type is also a pure race, but it is one which had only a little red at the margins of the petals and a type to which de Vries gave the name Delilah. The ninth type is also a pure race, which has white flowers and is like the pure white parent used in the cross.

De Vries states that in the reds and the Delilahs found in F_2 there was a good deal of variation, which is what we might expect from the relations shown in Table II, but he was able to group them, as shown at the bottom of Table II, and get the usual Mendelian ratios.

I have assumed here that when the enzyme is present in proportions from 82 per cent. to 84 per cent. of that in the pure red race, we get the Delilah type. This merely means that in the Delilah types the amount of enzyme present is near the critical point for the production of red color. There seems to be no question that the environment in the organism itself is a very important determining factor in the development of any character. It is not therefore fanciful to assume that in view of the fact that we get color development only in the petals the tendency to color development might be greater in one part of the petal than in another. We thus see that our assumptions are in agreement with the facts of inheritance made out by de Vries.

Cryptomeric Characters

In one of Bateson's *Matthiola* crosses,[10] between a cream-colored and a white race, he found that the first cross was purple and that amongst its progeny it produced purples, reds, creams and whites. He explained these phenomena by assuming that red is due to two cryptomeric factors which are ineffective unless present in the same cell, while purple was due to a third factor which converted red into purple and which was found in the white variety. These phenomena may be brought in line with our hypothesis, as shown in Table III.

In this case we evidently have to deal with more than two chemical substances. For the production of the red character itself two of these substances are necessary. It is, of course, possible that in the simpler case considered earlier the same two substances, possibly others also, are responsible for red, but, there being a deficiency in only one of them, we get the phenomena considered in Table I.

---

[10] See Rep. III, Evolu. Com., Roy. Soc., 1906.

TABLE III

Cryptomeric Characters

Bateson's Matthiola Crosses

R_1 = first factor for red; R_2 = second factor for red.

P = factor for purple. R_1 and R_2 produce red when present in greater proportion than 90 per cent. of normal amount in pure purples.

P converts red to purple when P is present in 90 per cent. of normal amount in pure purples.

Organs.	Cream var.			White var.			F_1		
	R_1	R_2	P	R_1	R_2	P	R_1	R_2	P
	%	%	%	%	%	%	%	%	%
Cy	18	20	24	18	20	24	18	20	24
AA	*12*	26	26	28	26	26	*20*	26	26
BB	14	16	12	14	16	12	14	16	12
CC	22	20	22	22	*2*	22	22	*11*	22
DD	18	18	*0*	18	18	16	18	18	*8*
	84	100	84	100	82	100	92	91	92

In the cross now under consideration we must assume that, taking the cream and the white races collectively, there are deficiencies in two substances necessary for the production of the red, as well as in the substance necessary for the production of the purple, or in one of the substances if more than one is necessary.

Let R_1 represent the first factor for red, R_2 the second factor for Red, and P the factor for purple. It is assumed that when either R_1 or R_2 is deficient to the amount of 10 per cent. of the amount of these substances found in pure purple races, the reactions will not reach the stage necessary for the production of red color, and that when there is a like deficiency in the substance necessary for transforming red into purple this transformation does not occur.

Column 2 of Table III shows the contribution of each of the cell organs to the substance R_1 in the cream variety; the next column gives similar data for substance R_2, and the next for the purple factor. The facts indicate that there is a deficiency in one pair of chromosomes (AA) for the substance R_1 in the cream variety; also for the purple factor in another pair of chromosomes (*DD*). These deficiencies are italicized in the table. In the white variety there is assumed to be a deficiency for the substance R_2 in a third pair of chromosomes. These assumptions give the phenomena found by Bateson. A similar case is found in sweet peas.[11]

It is seen in Table III that the cream variety has less of R_1 than is necessary to produce red coloration. It also has less of the purple factor than is necessary for converting red into purple, while the white variety has less of the substance R_2 than is necessary for the production of red.

Generation F_1 will have enough of all these substances to produce red and to convert red into purple.

The second generation of this hybrid contains 27 types. I will not here go into detail concerning that generation, but will merely add that the assumptions made are consistent with the facts observed in the second generation.

TABLE IV

HETEROZYGOTE CHARACTERS

Spotted F_1 beans from non-spotted P_1's.

S_1 = first factor of spotting; S_2 = sec. factor of spotting. S_1 and S_2 assumed to become operative when present in greater proportion than 85 per cent. of normal in pure spotted beans.

Organs.	♂ Parent.		♀ Parent.		F_1	
	S_1	S_2	S_1	S_2	S_1	S_2
	%	%	%	%	%	%
Cy	40	30	40	30	40	30
AA	36	*22*	*16*	42	*26*	*32*
BB etc.	24	28	24	28	24	28
	100	80	80	100	90	90

Table III deals with cryptomeric characters which are seen to owe their development to the reaction between two, or possibly more, chemical substances, the production of each of which is a generalized function of the cell. It is, of course, possible that each of these substances is produced only by a single chromosome, which case would be merely a limiting case in which all the cell organs except one produce none of a given substance in question.

---

[11] Rep. III, Evolu. Com., Roy. Soc.

Table IV deals with that class of characters which appear in heterozygotes, but not in pure races. Loche, Von Tschermak, Shull and Emerson have all studied such a character in beans. In certain crosses between beans not having spotted seeds the heterozygotes were spotted. Let us assume that the development of spotting on the seed coat is due to certain metabolic activities that involve at least two substances the production of which is either a generalized function of all cell organs or is a function of at least one pair of chromosomes. Let S_1 represent one of the substances necessary to these reactions, and S_2 another. Further, let us assume that in order to bring about the conditions necessary for the reaction both S_1 and S_2 must be present in a proportion 85 per cent. as great as in pure races of beans with spotted seed coats. In one of the races we assume a deficiency of substance S_2, and we assume that this deficiency is found in one pair of chromosomes only. In the other race there is a deficiency in substance S_1, and the same pair of chromosomes is responsible for this deficiency. Column 3 of Table IV shows 80 per cent. of the amount of S_2 found in ordinary spotted races of beans, while column 4 shows a similar deficiency in the substance S_1 in the other race.

Now generation F_1 of this cross receives one of the chromosomes in question from each of the parents, and in the case of each substance there is a deficiency of only 10 per cent. This gives us a spotted seed coat.

In the second generation, which is not shown in the table, one fourth of the progeny would be like the male parent and the other fourth like the female parent, neither of which has spotted seed coats, while half of the progeny would be like F_1 with respect to spotting of the seed coat.

While in this discussion it has been assumed that each of the substances with which we dealt was produced as the result of a general function of protoplasm, this is not necessarily the case. When we consider the history of the chromosomes it would appear very reasonable to suppose that marked variation in the composition, and consequently in the functions, of the chromosomes may have occurred as a result of evolutionary changes. It may be that some of the substances with which we have dealt are produced only by particular chromosomes, but we can hardly decide this question with the evidence at hand. In any case, particular chromosomes must be responsible for the deficiencies of the substances in order to get Mendelian phenomena. As previously stated, my object is simply to show that it is possible to make assumptions that will give us Mendelian phenomena without unit characters. The assumptions made seem to be consistent with the facts of physiological chemistry.

Even if we assume that the various substances with which we have been dealing are each produced by a single pair of chromosomes rather than by all the organs of the cell we can not look upon the chromosomes as the hereditary units spoken of by the de Vriesians and Weismannians, for we here look upon each chromosome as playing possibly an important part in the development of every feature of the organism.

The fact that in some species the number of pairs of Mendelian characters found is greater than the number of chromosomes is not an argument against the validity of the assumptions I have made. In Table IV we have assumed that the same pair of chromosomes may be responsible in one race for the deficiency of a certain substance and in another race for the deficiency of another substance. It happens in this case that the two substances concerned are both necessary to a particular reaction. If each chromosome play its part in the development of all parts of the organism, we might, in different races of a species, have a good many Mendelian characters dependent upon the same set of chromosomes, and instances of this kind are not wanting. For instance, Bateson found a particular flower color and a particular shape of the standard in sweet peas to be alternative to each other in inheritance. In other words, in the terms of our theory we have here two pairs of Mendelian characters based on the same pair of chromosomes. Several other similar cases are known. So that in order to prove that anything smaller than a chromosome is responsible for a Mendelian character difference it must be shown that we can get into a single individual more independent Mendelian character pairs than it has pairs of chromosomes. Both Baur and Shull, in private correspondence with the writer, have admitted the justice of this contention, and have promised to put it to the test.

Under the present hypothesis what has heretofore been called a pair of Mendelian unit characters must have a new name. For instance, in the red and white pea cross, if our assumption regarding the cause of the Mendelian phenomena is correct, we are not dealing with a pair of characters at all in the de Vriesian sense. Red is assumed to be a generalized function of the cell, and white likewise, but the difference between the red and the white concerns a single cell organ, and it is this difference with which we are dealing. Dr. McDougal, in conversation with the writer on this point a few days ago, suggested that in discussing this hypothesis we use the term "character differential" instead of character pair, and the suggestion seems to be a good one. We do, however, need a few terms, which I shall now proceed to introduce Under our hypothesis each of the organs of the cell is supposed to have various functions in development. One function may relate to the development of a particular character, and another to a very different character. Furthermore, several or all the organs in the cell may each have a function relating to the same character.

But not only are the organs of the cell supposed to play their part in development, but various organs, tissues and substances produced in the organism during development may also have functions which play a part in the development of various portions of the organism. For instance, hairs normally develop only in the skin. Hence the skin itself influences the development of hair. It is supposed that certain substances, called hormones, may materially affect the development of parts of the organism widely separated from the part of the organism in which these substances are produced. Thus the greater development of horns in the males of certain species is supposed to be due to hormones produced in the testes.

Any organ, tissue, substance or cell organ which thus has the power of influencing the course of development, I propose to call a "teleone." This word is from the Greek *teleo,* which means *make,* or *accomplish.* Teleones occurring in the egg, and presumably derived directly from the previous generation, may be called primary teleones. Those that arise during the course of development may be called secondary teleones. The manner in which primary teleones function in heredity has already been indicated. In a simple Mendelian character difference we are thus dealing, not with two unit characters, nor with the presence and absence of a single unit character, but with a difference between two teleones.

Under this hypothesis, transmission becomes, not the transmission of characters as such, but the transmission of cell organs having functions which determine character, or which influence development. This hypothesis may properly be called the teleone hypothesis.

A word about species crosses. We may imagine that, in species not closely related, the corresponding teleonic functions all differ more or less; hence we should not expect many simple Mendelian phenomena in such crosses. Again, in wide crosses, it will probably happen frequently that the chromosomes brought together will be so dissimilar that they do not act together in the usual manner, especially in the reduction division. We should expect Mendelian phenomena only in cases where homologous chromosomes go through synapsis and reduction in a formal manner.

Finally, when character differentials relate to anything other than chromosomes, Mendelian splitting should not occur. I would therefore suggest that some of the character differentials studied by Castle in rabbits are due to cytoplasmic differences, or at least are not due to the chromosomes.

THE EVOLUTION OF NEW FORMS IN VIOLA THROUGH HYBRIDISM[1]

PROFESSOR EZRA BRAINERD

MIDDLEBURY, VERMONT

DURING the past eight years I have given much time to the study of our North American violets, not only as represented in large herbaria, but especially as seen in living specimens, both in their natural surroundings and under culture. My garden now contains over 3,500 violet plants of about 650 different numbers or sorts, some 200 of which are from the wild, and 450 raised from seed.

The genus has for over a century been known as difficult and perplexing because of its polymorphism. It has been my good fortune to discover that this is largely due to the frequent occurrence of hybrids between species of the same group. I make out to date some 66 different hybrids that have arisen spontaneously. From about 50 of these I have raised offspring that segregate, often in a surprising manner, reverting variously to the characters of the putative parents of the hybrid. In many cases I have raised from the hybrid two, or even three, generations of offspring.

But not all the anomalous violets that I have grown and propagated can be called hybrids. Hybrids in *Viola* may be known by two marks: first, they are either completely sterile or markedly infertile; secondly, their seedlings are strikingly unlike each other, and often unlike the mother plant. The other class of anomalous violets are normally fertile, and come true to seed; they are often of sporadic occurrence, or if appearing in two or three stations, the stations may be hundreds of miles apart; furthermore, they usually present a mixture of the characters to be found in some two of the species with which they grow. These odd forms, of which I have noted nearly a hundred, are, in my opinion, largely the *result* of hybridism in the remote or recent past. The detailed evidence of this can not be presented in a twenty-minute paper; it demands a printed essay with abundant illustration. I shall here attempt only a brief summary of methods and results.

---

[1] This paper was presented before the American Society of Naturalists, in Boston, Mass., December 29, 1909.

I would first call attention to the transitory existence of a hybrid, especially when self-fertilized, as is usually the case in *Viola*. This follows from the laws of Mendel as a mathematical corollary, though I am not aware of any paper in which these deductions have been clearly set forth. Mendel, indeed, showed that in the case of the monohybrid (where the parents differ in only one character) the offspring in the first generation are one half stable, in the second three fourths stable, in the third seven eighths, and so on; until in the tenth generation there is on the average only one hybrid in 1,024 plants. But it can be proved that where the parents differ in *two* characters there will be on the average in the tenth generation only two hybrids in 1,024 plants; where the parents differ in three characters, there will be less than three hybrids in 1,000 plants: where they differ in four characters, less than four hybrids in 1,000; and so on. In the ordinary hybrid over 50 per cent of the offspring in the fourth generation will be stable; in the sixth generation over 85 per cent will be stable; in the eighth generation over 95 per cent; in the tenth generation over 99 per cent. The life of the self-fertilized hybrid is therefore always precarious and relatively brief. The organism is in unstable equilibrium, and is rapidly shifting into conditions of stability.

But the stable forms that emerge are not, as a rule, the forms found in the parents of the original hybrid. They are exclusively such only in the case of the monohybrid; in hybrids of a higher grade the stable forms consist of all possible recombinations of the opposed characters of the parent species. Two species that differ in six characters are capable when crossed of giving rise to 64 distinct and stable forms; if they differ in eight characters, of giving rise to 256 stable forms; if in ten characters, of giving rise to over 1,000.

One or two particular cases must suffice to illustrate how new and stable forms are artificially produced by the propagation of hybrid offspring. In September, 1905, with Mr. Witmer Stone, of Philadelphia, I visited Ivy Hill Cemetery, an interesting violet station, from which the previous May he had sent me several anomalous forms of *Viola.* Two of these proved to be hybrids of a species since named *V. Stoneana;* one with *V. papilionacea,* and the other with *V. triloba. V. Stoneana* has palmately dissected leaves and light-yellow seeds; *V. papilionacea* has undissected leaves, and dark-brown seeds. Among the progeny of their hybrid has appeared a form with the undissected leaves of *V. papilionacea* and the light-yellow seeds of *V. Stoneana.* This form comes true to seed (as was to be expected, since both characters presented are recessive), and shows no longer any marks of hybridity or infertility. Thus has appeared in the garden a stable variety of *V. papilionacea* with light-yellow seeds.

In the second hybrid, *V. Stoneana* × *triloba,* both parents have dissected leaves, though of unlike pattern; but *V. triloba* differs from *V. Stoneana* in being markedly pubescent. The first sowing of the hybrid seed gave me only four plants, one quite glabrous, three quite pubescent. Seeds of these were sown the following year, and from one of the three pubescent plants were obtained nine offspring, all pubescent with the leaf-form of *V. Stoneana.* So here we seem to have a pure dominant—a stable exhybrid—a new and pubescent variety of *V. Stoneana.* Just such a plant was once sent me by Mr. House, collected in the vicinity of Washington.

Leaving now the many cases of dehybridization in *Viola,* that have arisen in a few years of garden culture, let us glance at the evidence that this same process is going on in a state of nature, and has probably been going on for centuries.

Viola cucullata is a well-marked species of wide distribution, but it exhibits many anomalous forms; or as some would say, it is "an aggregate species." The capsules are a clear green in the numerous specimens that I have seen, with one exception. A plant, sent me by Miss Ryon from East Lyme, Conn., has dark-purple capsules; it is quite fertile, breeds true to seed, and in all respects but capsule color is normal *V. cucullata*. How shall we account for this aberrant form? Fortunately, with this plant was sent also from the same colony a hybrid of *V. cucullata* × *sororia*. The latter species at this station, as often elsewhere has very dark-purple capsules; may we not reasonably believe that the purple-fruited *V. cucullata* is a Mendelian product of the hybrid with which it was growing?

Viola cucullata is normally a very glabrous plant. But I have received forms of *V. cucullata* that were decidedly pubescent, from three widely separated stations: Mt. Mitchell, N. C., Milwaukee, Wis., and Salamanca, western N. Y. The plant from Wisconsin has a roundish leaf that resembles that of *V. sororia,* a pubescent species found at the same station. It is quite likely, therefore, that both the leaf-outline and the pubescent peduncles of the aberrant plant have come about through a former cross between the two species.

In October, 1906, I received indirectly from Miss Mulford, of Hempstead, Long Island, a plant of *V. affinis* that had black seeds. The species, which is as widespread as *V. cucullata,* has normally pale-yellow seeds. I noticed that the black seeds of Miss Mulford's plant were also somewhat larger than the ordinary yellow seeds of *V. affinis*. A careful weighing of 200 well-dried seeds of each lot shows the black seeds to be 49 per cent. heavier than the yellow seeds. I surmise, therefore, that the anomalous form is a by-product of *V. affinis* × *papilionacea,* a hybrid from which I have obtained forms in the garden similar to Miss Mulford's. I should add that though the black seed-color is dominant over the pale yellow, two generations of offspring from the Mulford plant show the black color to be stable.

Just the opposite effect has been brought to pass in certain plants of *V. nephrophylla,* a northern species ranging from eastern Quebec to the Rocky Mountains, and having black seeds in all the many specimens seen, except the one here discussed. This plant with buff seeds appeared in a parcel of *V. nephrophylla* sent from Lake Nemahbin, Wis., in 1907, by Dr. Ogden, of Milwaukee. The plant was in all other characters good *V. nephrophylla;* the capsules were crowded with seeds which for two generations have in turn produced plants with like buff seeds. Now from the same region Dr. Ogden sent me a few days later the hybrid *V. affinis* × *nephrophylla,* seeds from which the following year gave plants with buff as well as with black seeds. It is therefore probable that the fertile and stable buff-seeded *V. nephrophylla* from Lake Nemahbin is the descendant of a hybrid of this species with buff-seeded *V. affinis.*

Many similar cases have come under observation. In a limited region in Salisbury, Vt., of less than a square mile, there occurs not infrequently a very pubescent form of *V. latiuscula,* a species which in all other stations I have found to be quite glabrous. On the other hand, from three stations I have obtained perfectly glabrous plants of *V. palmata,* a species normally pubescent. The plants from two of these three stations were somewhat infertile, thus betraying their hybrid origin.

The effect of hybridism is plainly to be seen in the numerous intergradient forms that occur between closely allied species of *Viola.* Take, for example, *V. fimbriatula* and *V. sagittata,* merged into one species by Dr. Gray, probably because of this intergradience. The extreme forms differ chiefly in three particulars: the leaf-blade of *V. sagittata* is narrowly lanceolate, glabrous and coarsely toothed at the base; that of *V. fimbriatula* is oblong-lanceolate, pubescent and not coarsely toothed at the base. But not infrequently we find colonies of *Viola fimbriatula* with leaves that *are* coarsely toothed at the base, and colonies of *V. sagittata* with decidedly pubescent leaves; indeed, this is the prevalent form in the middle west. Where the two species grow together, these and various other interchanges of characters are frequent, in accordance with Mendelian principles of segregation. A like interchange of characters is noticeable in the stemless white violets, *V. blanda, V. renifolia* and *V. incognita;* and also in the stemmed yellow violets, *V. pubescens* and *V. scabriuscula.*

We often find in species of wide distribution, as for example *V. affinis* or *V. papilionacea,* numerous forms distinct in one or more characters. Those who are so inclined can break up any one of these species into a dozen or more "elementary species," as some European botanists have done with *V. tricolor.* But there are also certain species of *Viola* that are not polymorphic though of fairly wide distribution; for example, *V. rotundifolia, V. Selkirkii, V. hastata;* and it is worthy of note as bearing upon the thesis of the present paper, that these species have never been found to hybridize.

It frequently happens that a subhybrid form in *Viola* is so unlike either parent of the first-cross as to appear to be specifically distinct. Many such violet hybrids have in recent years been named and published as species: *V. Mulfordæ* Pollard, *V. notabilis* Bicknell and *V. aberrans* Greene are examples. It is surely hazardous in our present knowledge of the genus to put forth as a species a newly discovered form of *Viola,* without studying it through at least one season of growth and through one generation of offspring. It may, indeed, transpire that the new form, though of hybrid origin, is distinct and stable; and if fairly wide-spread, it may be entitled to specific or varietal rank. The bar sinister in the escutcheon of its bastard ancestry may have been quite obliterated. We may be here witnessing the birth of a new species through hybridism. Allow me in closing to present an instance that makes a close approach to these conditions.

In May, 1906, Mr. Stone sent me from Tinicum, Pa., a living violet plant that was quite fertile and appeared a good species. I could not make it out a hybrid, though perhaps predisposed at that time to place an anomalous form in this category. For further light I visited the station with Mr. Stone the following September; but the most careful search failed to reveal another specimen. It soon afterward occurred to me that it might be an offspring of *V. affinis* × *sagittata,* a hybrid which I had found at the same place the year previous, and had transferred to the garden. The two plants, mother and supposed daughter, appeared much unlike, the former being quite infertile, and in most respects an excellent intermediate between the putative parents that grew near by. But careful examination showed that, though no one character of the supposed daughter was intermediate as in the mother, yet *all* were to be found in one or the other of the supposed grandparents. The leaves had the breadth and the rounded basal lobes of *V. affinis,* but the length and the attenuate apex of *V. sagittata;* the capsules were pubescent as in *V. affinis,* but green and large as in *V. sagittata;* furthermore, the peduncles were strictly erect as in *V. sagittata,* not ascending as in *V. affinis;* and also the seeds were brown as in *V. sagittata,* not buff as in *V. affinis.*

The next move was to raise offspring of the plant, to discover if some one of these characters was not impure —in other words, dominant and holding latent the opposed character. The 23 plants subsequently raised showed all the characters of the plant under investigation to be pure excepting two, the pubescence of the capsules and the dark-brown color of the seeds; for glabrous capsules and buff seeds appeared in some of the offspring. The ratio of the four Mendelian forms in the 23 plants was 12: 4: 4: 3, or 9: 3: 3: 2¼, an unexpectedly close approximation to the theoretical ratio 9: 3: 3: 1.

From eleven of these plants another generation of 204 plants was raised the past season. Among these, in addition to the five possible hybrid forms, were obtained also the four possible stable forms. So that I now have fertile plants, free of all hybridity, of four sorts, viz., 18 with pubescent capsules and dark seeds, 9 with pubescent capsules and buff seeds, 18 with glabrous capsules and dark seeds, 44 with glabrous capsules and buff seeds.

Surely, what I have done in the garden, nature might do in the wild, thus evolving a distinct species with three varieties.

In justice to my subject let me say that I am far from maintaining that hybridism is furnishing in the genus *Viola* all the new forms for natural selection to work upon. Hybridism adds no new character to a group of species; it simply recombines in multifarious ways characters already existing. However numerous the patterns that appear in the revolving kaleidoscope, their number is limited; and if we looked long enough we should find them substantially recurring from time to time. To get a strictly new pattern, we should need to insert in the apparatus a new fragment of colored glass. In the evolution of living organisms the new piece of colored glass is what the biologists are considering under the name of mutation.

TERTIARY ARCHHELENIS

DR. A. E. ORTMANN

CARNEGIE MUSEUM, PITTSBURGH, PA.

THE *Archhelenis-theory* of von Ihering has now received so much support from various sides that we may regard it as firmly established with regard to its general correctness. Stated in broad terms, this theory assumes a former land connection between Africa and South America, which is rather old. This connection is the last remnant of a large southern continental mass (South Atlantis, Gondwana-land), which existed since the beginning of the organic history of the earth (Cambrium), which was broken to pieces at different times, and the remnants of which are now found in Australia, India, Africa and Brazil. The separation of Brazil from Africa was the last step in the dismemberment of this old continent, an event which is placed by most writers toward the end of the Mesozoic era, although some have admitted the possible continuation of Archhelenis into the beginning of the Tertiary.

Recently, von Ihering has tried to fix the time of the disappearance of the connection between Africa and Brazil more exactly, and arrived at the conclusion that Archhelenis *persisted* at least through the *Eocene*. He discusses the question chiefly in connection with his studies on the marine fauna of the Patagonian beds, which he regards as Eocene.[1] Comparing this fauna with the contemporaneous Tertiary faunas of the rest of the world, he discovers certain facts, which, according to him, can not be explained except by the assumption that Archhelenis was still in existence at the beginning of the Tertiary.

---

[1] Ihering, H. von, "Les Mollusques fossiles du Tertiaire et du Crétacé supérieur de l'Argentine," *Anal. Mus. Buenos Aires*, 14, 1907.

I fully accept the facts of the faunistic relations of the Patagonian beds, as laid down by von Ihering. Yet I do not believe that they demonstrate the necessity of assuming the existence of Archhelenis at that time, but, on the contrary, I believe *that they point just to the opposite,* namely, that at the time when the Patagonian beds were deposited (in the early Tertiary—it does not matter, for the present purpose, whether we regard the beds as Eocene or younger) the connection between Brazil and Africa must have disappeared, and that there must have been a deep ocean in its place.

Of the relations of the Patagonian fauna to other faunas, the following are mentioned by von Ihering as most important (p. 76 ff.).

While the Patagonian fauna in general is very peculiar, and consists preeminently of southern (antarctic) elements, yet there are certain affinities to Tertiary faunas of the northern hemisphere. But there are hardly any relations to North America, and the few affinities with northern faunas are rather with the *Indo-European fauna.* This, of course, means that the Indo-European forms, which may be regarded as constituting resemblances with the Patagonian fauna, are *not* found in North American Tertiaries. Von Ihering believes that these peculiar conditions are to be accounted for by the existence of a land barrier between the North and the South Atlantic, which prevented a migration of North American marine forms to Patagonia, while there was a possibility for Patagonia to receive Indo-European types from the Indian ocean along the eastern coast of Africa and the southern coast of the Atlantic land-connection (Archhelenis).

While I do not doubt the correctness of the view that Patagonia did not receive the Indo-European elements of its fauna by the direct way, from the Mediterranean across the Atlantic, I think, the fact of the *absence* of these forms from North America is not correctly understood and interpreted by von Ihering. If Archhelenis existed at that time, there must have been *a coast line* not only in the south, but also in the north of this land, *running across the present Atlantic from North Africa to the West Indies.* Since the forms under discussion are most emphatically marine littoral-shells, such a coast line would have favored their migration from the European waters to those of the West Indies and North America. Thus these forms, which are found both in the Patagonian and in the Indo-European Tertiaries, should have been able, by all means, to reach also North America. The fact, however, that they are absent in the latter parts indicates decidedly, that there was no possibility for them to go across the Atlantic from Europe to America, and thus there can not have been a coast line or a land connection between Africa and South America, but there must have existed a deep ocean (the Atlantic), which prevented their migration from Europe to North America as well as from Europe by the direct way to Patagonia.

One fact, however, remains now unexplained, namely, the absence of North American types in Patagonia. If the Atlantic Ocean extended uninterruptedly from north to south, as it does now, there must have been, disregarding small interruptions at Panama and in the region of the Amazonas, a rather continuous shore line, along which the northern forms could have migrated to Patagonia. I think such a north-south migration actually took place, but it did not reach the southern extremity of South America on account of climatic differentiations along this coast line. Von Ihering points out (p. 492) that the Patagonian fauna is characterized by the absence of certain types of shells, which are preeminently tropical. This very strongly suggests that the Patagonian Tertiary seas were not of a tropical, but of a subtropical or even temperate, character. If this is true, it is apt to furnish an explanation for the absence of North American forms in Patagonia. The North American fauna of the Tertiary is found from Florida to New

Jersey, and some of the richest deposits are in Florida and Alabama, parts which surely had a tropical climate in the beginning of the Tertiary. If Patagonia was extratropical, we can not expect that this fauna should have reached it, for its southward migration would have been stopped by the southern boundary of the tropical belt.

On the other hand, von Ihering points out that, while there was no immigration of tropical West Indian and North American types during the Patagonian time, such an immigration took place later, when the Entrerios beds were deposited (which he believes to be Miocene), for we find such forms in these beds. He thinks that it is thus demonstrated that the destruction of Archhelenis falls in the time between the deposition of the Patagonian and Entrerios beds. I can not admit this, for the Patagonian beds are found far to the south (between 45 and 50° S. lat.), while the Entrerios beds are in 30–35° S. lat. It is true, there are localities for Entrerios beds farther to the south (as far as about 43° S. lat.), but of the characteristic tropical types, which are named by von Ihering (on p. 361) not a single one is found at these southern localities (see table on pp. 357 and 358). Thus it is very probable that, while at the time and the locality of the deposition of the Patagonian beds an extratropical climate prevailed, a tropical climate may have existed at the same time farther north (north of say about 40° S. lat.). However, we do not know the corresponding deposits of these parts, and we only know that there are tropical immigrants in later deposits in about 30–35° S. lat., but this does not prove that there were no such in the northern parts of Argentina at the time of the deposition of the Patagonian beds. In fact, the presence of certain tropical types in the Navidad beds of Chile (p. 514), which very much resemble the Patagonian beds in general character, but are situated a good deal farther north, suggests strongly, that the Navidad beds are the tropical "facies" of the Patagonian beds. I do not think that a separation of the Patagonian and Chilean sea by land is to be assumed for the explanation of the absence of these tropical types in the Patagonian beds, as von Ihering is inclined to do (p. 495). Of course, the Patagonian beds were deposited on the east side, those of Navidad on the west side, of the old peninsula extending northward, and now represented by the Chilean Coast Cordilleras, but this peninsula had an end somewhere to the north, and around this point a communication of the two seas was possible, till the elevation of the Cordilleras de los Andes took place, and connected the old Chilean land with the land lying to the east of it.

Further, if there was no connection of Africa and Brazil any more in Tertiary times, the migration of the Indo-European forms to Patagonia by the route indicated above (East Africa, and south coast of Archhelenis) was impossible. Yet there is another way open. As von Ihering points out (p. 81), this Indo-European fauna reached eastward to Australia and the Pacific Islands, and thus it very likely does not originally belong to the fauna of the old Tethys (Mediterranean, North Atlantic, West Indian seas), but consists of old Pacific elements which extended, in the Tertiary, eastwards into the Mediterranean part of the Tethys (Europe). The very absence of these types in the West Indies and in North America supports this view. And further, since the Antarctic fauna, to which the Patagonian fauna shows the closest affinities, is nothing but an offshoot of the old Pacific fauna, the relations of the Patagonian to the Indo-European forms find thus their explanation, and the way, by which these faunas are connected, apparently goes over Australia and Antarctica.

Finally, for the non-existence of Archhelenis in the Eocene very recently a new line of evidence has been introduced. Stromer[2] points out that recently quite a number of marine Eocene deposits have been discovered in West Africa, namely, in the region south of Senegambia; on the middle Niger River; in the southern central Sahara and in northern Nigeria; in Togo and Cameron (Gulf of Guinea); and even as far south as the Gabun, Angola and Mossamedes. Although these deposits are rather scattered, their Mediterranean character has been recognized, so that it appears as very probable that they belong to a continuous sea, which extended south from western Europe along the west African coast. That is was actually continuous is demonstrated, according to Stromer, by the distribution of the Nummulites in these beds, which are found only in the north, and indicate a cold northward current along the west African coast: such a current could develop only under a similar distribution of land as at present, namely, if the west African coast extended uninterruptedly from south to north, as it now does. This, of course, would show that the Atlantic at that time existed approximately in its present form, its northern (Tethys) and southern (Nereis) parts being connected, and that the separating land bridge, Archhelenis, had disappeared.

---

[2] Stromer, E., "Ueber Alttertiaer in Westafrika und die Suedatlantis," *Jahrb. kgl. Preuss. Geol. Landesanst.*, 30, 1909, p. 511 ff.

All the above considerations lead us only to one conclusion: that *in the beginning of the Tertiary Archhelenis had ceased to exist, and that there was no connection any more between South America and Africa.* Indeed, the facts introduced by von Ihering in support of his assumption of the existence of this land-bridge in the Eocene, prove to be, under renewed critical investigation, *the strongest evidence for the contrary,* and it has been shown above that also some other facts, which apparently contribute to the support of von Ihering's view, may be easily understood under the assumption that *Archhelenis had been destroyed at the beginning of the Tertiary time.*

SHORTER ARTICLES AND DISCUSSION

THE PROBABLE ORIGIN OF THE CRINOIDAL NERVOUS SYSTEM

Although at first sight the nervous system of a crinoid appears to be so radically different from that of an invertebrate of the more usual bilateral type that no satisfactory comparison is possible between them, I believe that there is no difficulty at all in deriving it from the latter.

The nervous system of a crustacean, worm or insect consists typically of a supraœsophageal ganglion united by a pair of circumœsophageal ganglionic connectives to a more or less marked subœsophageal ganglion, from which there runs back along the ventral side of the animal a long nerve cord, or pair of nerve cords, marked at intervals with ganglia. The anterior end of the digestive tube passes between the two chief ganglionic masses, as the names of all these structures indicate.

The ancestral crinoid was bilateral, and therefore possessed a nervous system constructed according to this plan. With the progressive decrease in directive locomotion the ventral nerve cord was correspondingly shortened, concurrently with the assumption by the animal of a more compact form, just as the nerve cord has been shortened in *Cancer* as compared with *Palinurus,* in *Dynamine* as compared with *Apseudes,* in *Cimex* as compared with *Diapheromera,* or, better, in the crustaceans as a class as compared with the annelids as a class. In the crinoids the shortening progressed still further; locomotion, other than casual or accidental, ceased; the anterior end of the intestinal canal became deflected upward and pressed upon the anterior part of the supraœsophageal ganglion which gave way before it and became deeply crescentic; at the same time the ventral nervous cord was retracted into a short protuberance from the subœsophageal ganglion. Finally the horns of the crescent formed from the supraœsophageal ganglion met in front of the throat so that what was originally a ganglion mass became a nerve ring, the two connectives became broken up into numerous connecting fibers, and the whole ventral nerve cord with its ganglia became retracted into the subœsophageal ganglion, now become the dorsal nerve mass.

Thus we may very easily derive the radiating nervous system of the crinoid from the bilateral nervous system of the arthropod, the circumoral nerve ring of the crinoid being derived from the supraœsophageal ganglion of the arthropod, and the dorsal nervous system from the subœsophageal ganglion. In this connection it is significant that the circumoral nerve ring innervates the same structures and possesses the same functions as the supraœsophageal ganglion, while the dorsal nervous system is identical with the subœsophageal ganglion, plus the ventral nerve cord, in the nature of its duties.

The assumption of the pentaradiate form by the crinoids has produced a complex condition of orientation; for the so-called "ventral" surface of the crinoid, in terms of arthropod or annelidan orientation, is equal to the anterior end, plus the posterior end, and plus such part of the dorsal surface as is not shoved to one side by the approximation of the two extremities of the intestinal canal; while the "dorsal" surface of the crinoid is the equivalent of the entire *ventral* surface of the arthropod, plus more or less, possibly nearly all, of the dorsal surface.

AUSTIN H. CLARK.

NOTES AND LITERATURE

RECENT LITERATURE TOUCHING THE QUESTION OF SEX-DETERMINATION

In 1889 Geddes and Thomson in their book on the "Evolution of Sex" stated that "Nutrition is one of the most important factors in determining sex" (p. 47), and developed the theory that "Anabolic conditions favor the preponderance of females, katabolic conditions tend to produce males" (p. 47). In the revised edition of 1901 practically the same idea is stated thus: "The female is the outcome and expression of relatively preponderant anabolism, and the male of relatively preponderant katabolism" (p. 140). The following year (1902) Beard[1] expressed the conclusion, based upon considerable evidence, that: "Any interference with, or alteration of, the determination of sex is absolutely beyond human power. To hope ever to influence or modify its manifestations would be not less futile and vain than to imagine it possible for man to breathe the breath of life into inanimate matter" (p. 763).

The two fundamental ideas here expressed—namely, that the nature of the environment (chiefly the amount of nutrition) may determine the sex of the developing germ, *i. e.*, that sex is quantitatively determined; and that sex is predetermined in the germ, *i. e.*, qualitatively (independently of external conditions if only they be favorable to development) have until recently sharply divided investigators on the problems of sex. Both positions seemed about equally well supported by numerous facts both experimental and cytological for animals, and experimental for plants. In only a few instances has opinion been divided over the same form; in the majority of cases the results appeared convincingly in favor of one or the other view.

The more recent tendency seems to be to interpret sex-determination (at least proximately) as the result of a quantitative relation between karyoplasm and cytoplasm in the fertilized ovum, or more strictly, between chromatin and cytoplasm. This position rests upon the observation chiefly that in those insects where heterochromosomes have been described the eggs which develop into females contain the greater amount of chromatin material (exceptions—*Metapodius*, Wilson: and possibly *Acholla*,

---

[1] Beard, John, "The Determination of Sex in Animal Development," Jena, 1902.

Payne), and has been suggested as probable more particularly by Morgan and by Wilson. The former,[2] however, regards the quantitative interpretation of sex-determination as only the "first rough approximation" (p. 348) to the solution; and the latter[3] inclines to the belief that "if the idiochromosomes be sex-determinants their difference is probably a qualitative one" (p. 189), though this may possibly be a difference merely of degree of special activity.

Boveri's[4] generalization that the cytoplasm and nucleoplasm of cells bear to each other a constant ratio, and that "a fertilized egg that contains more chromatin is a potentially larger cell than one with less chromatin" (pp. 9–10) may help to reconcile the conflicting theories. If the amount of chromatin may be rightly taken as an index of the state of nutrition or potential anabolic capacity, the apparently contradictory facts that nutrition (environment) in one case and internal factors (perhaps simply more or possibly more active chromatin) in the other case determine sex, can be harmonized. If chromatin and chromatic substances (nucleo-proteids) may be regarded as food material or active agents in constructive metabolism, the better nourished gametes (or such as contain more chromatin) appear destined to produce the female sex, the less well nourished the male sex.

Several recent investigations again affirm the opposing views, well supported with experimental or cytological facts, though a reconciliation is suggested from both sides on the basis of a quantitative relationship signifying in one direction high metabolism (anabolism) and in the other low metabolism ("relatively preponderant katabolism").

The most important recent paper concerning the question of the determination of sex is that of Russo.[5] This author takes issue with the prevailing hypothesis which views the chromosomes as the vehicles of the determinants of hereditary characters, and objects more especially to a Mendelian interpretation of sex-phenomena. The fact that in the gametes, particularly the eggs, besides certain phosphorus-containing proteins, lecithin is abundantly present, suggested a series of experiments to determine whether the lecithin content of eggs could be artificially increased and whether such accession could produce a significant physiologic modification in the germ-cells.

---

[2] Morgan, T. H., "A Biological and Cytological Study of Sex Determination in Phylloxerans and Aphids," *Journ. Exp. Zoöl.*, Vol. 7, no. 2, 1909.

[3] Wilson, E. B., "Studies on Chromosomes, V." *Journ. Exp. Zoöl.*, Vol. 6, no. 2, 1909.

[4] Boveri, Th., "Ueber Beziehungen des Chromatins zur Geschlechts-Bestimmung," *Sitz. Phys. med. Gesell. Wurtzburg.*, Jahrgang 1908–1909.

[5] Russo, A., "Studien ueber die Bestimmung des weiblichen Geschlechtes," Jena, 1909, pp. 1–105.

Russo finds that normally in rabbits and various other mammals the lecithin content of eggs of the same ovary varies greatly; some containing much, others little. This variable cell condition indicates a shifting chemical state, expresed morphologically in the form of "chromidial-bodies" (mitochondria, chondriomites, pseudochromosomes, chromidial net, etc.). These structures Russo has succeeded in producing by artificial means (*i. e.*, injection of lecithin), and he regards them as having "no small influence on developmental phenomena." He does not deny that the nuclear chromatin plays an important rôle in development, but he refuses to regard it as alone the material basis of heredity. The nuclei may assist in the process of heredity, but the results of his investigations on rabbits indicate that sex and other "unit characters" (*e. g.*, pigmentation) are a function of the degree of cell metabolism.

Russo believes that "contrary to the chromosome theory, the characters of Mendelian hybrids in the first or dominant generation, especially as concerns the pigmentation and color of the hybrid, do not bear any absolute relation to the chromosomes, but that they depend in greatest part upon a specific metabolism or chemical condition residing in the egg cytoplasm; that, further, the sex of the offspring depends upon a special metabolism (Stoffwechsel) of the germ-cells, and that by artificial modification of the chemical or metabolic state (Metabolismus) of these elements the Mendelian law (*i. e.*, of dominance) can be modified in that one may fix this or that most recent variety, as it is also possible at will to determine the sex" (p. 4).

Lecithin was administered subcutaneously, intraperitoneally and per os. The ovaries of lecithin-fed rabbits attained a size three times as great as that of ordinary individuals and contained much larger Graafian follicles. Under such treatment the germ cells became markedly anabolic. Russo notes that in normal ovaries some ova contain much deutoplasmic material in the zona pellucida and the vitellus, and others little or none. The artificially highly nourished eggs produce females; and the lecithin-fed individuals give rise preponderatingly or even exclusively to female offspring. There are thus in rabbits two kinds of eggs corresponding, respectively, to each sex: (1) well nourished, highly anabolic, or female; (2) poorly nourished, slightly anabolic (or katabolic) or male.

The sperm, containing chemical substances similar to the eggs, are regarded as merely giving aid in the development of a process already begun in the egg leading towards the determination of a particular sex. That the sperm has a complementary and not an antagonistic rôle in sex-production seems established by the fact that the percentage of female offspring is higher when both male and female have been subjected to the lecithin treatment before union.

For the experiments Russo employed selected and ordinary varieties of rabbits. His chief aim was to "fix" a particular "unit character" of the female in the offspring (mostly female) of the first hybrid generation. The character selected was the color of the hair. Females of recent races characterized for hair color, *i. e.,* white (albino, Himalaya, Angora, etc.), were crossed with males of various phylogenetically older races (*e. g.,* "Grigia"—gray, and "Nero"—black). The best results were obtained from crosses between Himalaya females and "Nero" males. On crossing females of either albino or Himalaya races with males of "Grigia" and "Nero" stocks the offspring of the first generation always had the color of the male, *i. e.,* gray or black, respectively, showing that these crosses ordinarily conform to the Mendelian law of dominance. Moreover, Russo notes that in nature the number of male offspring always exceeds that of the female, the percentage of the former being variously given as from 52 to 58 per cent.

When the same females were subjected to the lecithin treatment before conception, the offspring of crosses similar to the above were in the first generation preponderatingly of the type of the newer or female race. There frequently appeared atavistic exceptions, interpreted as due to a late ripening of the eggs concerned which consequently remained unaffected by the lecithin.

The most clear-cut result was obtained from the following experiment: A preliminary experiment, several times repeated, having shown that the ordinary cross conformed to the law of dominance, a young well-nourished "Polacca" (white) lecithin-treated female was crossed with a "Nero" male (black). The resulting progeny included 6 females (5 white) and 2 males (1 white), showing clearly that the female subjected to lecithin treatment yields a preponderance of females (with the maternal somatic character of hair color).

Occasionally the cross between a lecithin-fed Himalaya female and a normal "Nero" male resulted in several modified Himalaya offspring (*e. g.*, black legs or dusky coat, etc.) among the preponderating Himalaya hybrids. This condition is readily explained by assuming that in such crosses "the modification of the vitellus had not reached the necessary stage to impress upon the embryo the character of the maternal metabolism and with it the characteristic female features" (p. 16).

The cause of the concomitance of sex and particular somatic characters is believed by Russo "to depend upon a suitable modification of the germ-cell, related in some way to the age, the physiologic state and other conditions of the particular individual" (p. 98).

The evidence here appears unequivocal that external conditions (*e. g.*, nutrition) can determine the kind of sex and entirely vitiate the Mendelian scheme of ordinary crosses. Female sex and the maternal character of coat color moreover are shown to be associated with a more highly nourished egg, the artificially modified metabolism expressing itself in an abundance of deutoplasmic and chromatic substances (chromidial-net) in the zona pellucida and vitellus. The main stages in the chain of causes culminating in female sex seems to be, (*a*) high nutrition (lecithin), (*b*) increased size (preponderant anabolism), (*c*) storage of chromatin, (*d*) femaleness.[6]

A brief paper by Miss Boring[7] gives the results of a careful study of fertilized eggs of *Ascaris* with special reference to the small odd chromosome previously noted by Herla and later also by Boveri. This peculiar chromosome is said to be very rare in the variety *bivalens.* Its representative was never discernible in the oögonia and only very rarely in the spermatogonia. From observations of bastard eggs the conclusion is drawn "that the small chromosome surely comes from the spermatozoön in some cases, and possibly from the egg in others" (p. 125—one instance noted). The possibility is suggested that the small chromosome is a sex-determining heterochromosome; but Miss Boring has no doubt also that it is sometimes due to fragmentation.

---

[6] The relation of nutrition to sex-determination as demonstrated by Russo for the rabbit suggests a possible physiologic basis for the theory of sex-causation in man (based solely on clinical facts) as recently advocated by Dawson to the effect that females develop from eggs from the left ovary and males from eggs from the right ovary;—namely, that the permanent passive congestion in the left ovary, due to the entrance of the left ovarian vein at a right angle into the renal vein (whereas the right ovarian vein empties obliquely directly in the inferior vena cava) may produce a condition of relatively better nutrition. Cognizance must be taken of the fact, however, that the right ovary is frequently slightly larger than the left, a point which apparently contradicts the verity of this interpretation; but cytological investigation may reveal a better nourished condition of all of the ova of the left ovary, expressed in the presence of chromidal nets, etc.

[7] Boring, Alice M., "A Small Chromosome in *Ascaris megalocephala*," *Arch. f. Zellforschung.*, Bd. 4, H. 1, 1909.

Boveri[8] inclines to regard this fifth ("X")—chromosome of *Ascaris megalocephala bivalens* (present in approximately half the eggs) as comparable to the accessory chromosome of *Pyrrhocoris.* He considers it more probable that its occasional apparent absence (common condition in *univalens*) is the result of fusion with one of the other chromosomes, than that its presence is the result of fragmentation. He concludes that the "x-chromosome" appears to be an independent structure specific for the male sex—as was originally believed by McClung for insects. In analogy with conditions in insects (*e. g., Protenor*), Boveri assumes a dimorphism of spermatozoa, due to the presence of the x-element in half of the sperm and its absence in the other half. But the unfertilized eggs are supposed to have no homologous elements (there being no evidence of such structures); hence, contrary to his recent generalization that the female fertilized egg contained the greater amount of chromatin, the male sex here seems conditioned by, or concomitant with, a relative preponderance of chromatin. This contradiction is elucidated by facts discovered by Boveri and Gulick (*op. cit.*, p. 136) in a study of the spermatogenesis and maturation of *Heterakis,* a nematode of the pheasant. The spermatogonial cells have 9 chromosomes; the maturation spindles of the eggs 5. Two types of spermatids are produced, one with 4 the other with 5 chromosomes; and one kind of egg with 5 chromosomes. The condition is identical with that described by Wilson for the hemipter, *Protenor.*

These facts established for *Heterakis,* give a clue to the more probable state of affairs in *Ascaris.* Boveri reconciles the discrepancies by assuming a close union in the oöcytes of the homologues of the accessory chromosome with the other chromosomes thus masking their presence. In reality, then, *Ascaris mega-*

---

[8] Boveri, Th., "Ueber 'Geschlechtschromosomen' bei Nematoden," *Arch. f. Zellforschung.*, Bd. 4, H. 1, 1909.

locephala bivalens would have six (6) chromosomes in the female and five (5) in the male (apparently four (4) in each since the heterochromosomes commonly couple with the ordinary chromosomes).

The attempt to rationalize the assumption of such a union involves the hypothesis of chromosome individuality in extreme form, viz: "We can not doubt that also in the apparently homogeneous nucleus of the spermium each chromosome preserves its individuality; but all are most closely pressed together" (p. 139). The greater effort here demanded (as compared with the egg pronucleus) to separate the chromosomes in this more compressed condition affects also the odd chromosome and frequently disjoins it from its "companion."

Thus two more forms (from the group of the Nematodes) are shown to conform to Wilson's scheme of sex-determination. And though Boveri is forced to retract (p. 137) his former statement regarding a preponderance of chromatin in the female sea-urchin as judged from Baltzer's plates the evidence accumulates that the female sex is somehow associated with a greater amount of chromatin.[9]

In an extensive paper of 110 pages on sex-determination in *Polyps,* Nussbaum[10] describes in detail a large series of experiments extending from 1891 to 1897 on *Hydra grisea.* His discussion of results involves comparisons with the works principally of Krapfenbauer (*H. fusca*), Frischholz (*H. fusca* and *H. grisea*), Whitney (*H. viridis*) and Annandale (*H. orientalis*).

The aquaria were all arranged under similar conditions of light and heat; only the nutritive conditions were caused to vary by changes in the amount of food supply and by induced periods of budding. The temperature is said to have an effect on sex only indirectly through influence on the nutrition. In contradistinction to the four above-named investigators, Nussbaum maintains that the nutrition and not the temperature is the chief factor which determines change from the asexual or budding condition to the sexual (diœcious and hermaphrodite); though he agrees with the latter two that for each species there is a definite temperature-optimum.

[9] The case of *Acholla multispinoa* described by Payne (*Biol. Bull.*, Vol. 16, nos. 3 and 4, 1909) may perhaps prove a real exception, though it may be harmonized, as Payne suggests, by assuming a greater combined activity for the several smaller "differential chromosomes," than for the single absolutely larger male member.

[10] Nussbaum, M., "Ueber Geschleschtsbildung bei Polypen," *Arch. (Pflüger) f. Physiologie,* Dec. 30, 1909, Bd. 130.

With good feeding budding gives place to a sexual phase. On the basis of daily observations of many cultures for a number of years Nussbaum concludes that a more favorable nutritive condition produces the female polyp. "The mass of food governs budding and the production of sexual organs"—and the best nutrition produces females. The same polyp may enter upon repeated sexual phases each separated by a period of budding; but, while he seems to deem it possible, he has not yet succeeded in changing the sex of the same individual polyp directly into the opposite sex.

Here again the same general conclusion appears that sex is consequent upon the degree of nutrition and that the best nourished polyp produces eggs, *i. e.,* high nutrition conditions the female sex.

Nussbaum suggests an interesting new interpretation of hermaphroditism (gynandromorphism) among insects where a dimorphism of spermatozoa prevails, *i. e.,* where heterochromosomes are found. He believes it quite possible that occasionally the reducing division may be omitted in spermatogenesis and that the unmatured spermatocytes may develop directly into functional sperm. Shortly before, or at the time of, the first segmentation of an egg fertilized by such a spermatozoon, the male pronucleus is supposed to undergo its belated reduction division, one half (with the even number of chromosomes) passing to one daughter cell with one half of the developing egg pronucleus, and the other half (with the odd number of chromosomes) with the other similar half to the other cell. Thus would result a two-cell stage, one blastomere (female) containing one more chromosome than the other blastomere (male). If then, as has been experimentally demonstrated in several forms, each blastomere gives rise to one half of the resulting individual the symmetry of the insect hermaphrodite would be explained. Here again sex is thought of as determined by a quantitative relation of chromatin.

The results of the newer investigations on sex-determination seem, at least temporarily, to have brought us back to the position of Geddes and Thomson, namely, that femaleness is causally related to a dominating cell-anabolism and maleness to a relatively preponderant cell-katabolism. This conclusion would seem to be the base from which future investigations will start in the attempt to further elucidate the fundamental mechanism of sex-differentiation.

H. E. Jordan.

University of Virginia.

RECENT INVESTIGATIONS ON THE COMPARATIVE ANATOMY OF CONIFERS

Until quite recently there has been an increasing tendency to regard the two important coniferous tribes which are, at the present epoch, respectively characteristic of the northern and southern hemispheres, viz., the Abietineæ and Araucarineæ, as of different origin and not nearly allied with one another. This view of their derivation is, for example, represented by Professor Seward in his monograph on the Araucarineæ[1] and by Professor Penhallow in his "Manual of North American Gymnosperms."[2] A similar opinion has even quite recently been expressed by Mr. Thomson.[3] While the inferences of those whose conclusions are based almost entirely on a consideration of the structure of existing representatives of the Coniferales and of their surmised ancestors from the Paleozoic, have had the marked separatist trend indicated above, of late quite another tendency has made itself felt as a consequence of the structural investigation of the Mesozoic conifers and a comparison of these with existing tribes.

An important contribution on the structure of the Jurassic woods of King Karls Land[4] contains an account of a ligneous species, which the author names *Cedroxylon transiens.* This species is remarkable for the fact that it at the same time manifests the ray structure of the Abietineæ and in many instances the characteristic alternating radial pitting of the tracheids, which is a feature of the wood in existing Araucarineæ. On account of the latter feature Gothan, while referring the wood to the abietineous genus *Cedroxylon* Kraus, applies the specific appellation *transiens,* to indicate that in his opinion the wood in question marks a transition from the Abietineæ to the Auracarineæ. Of the general soundness of this view there can be no question. Nearly contemporaneously Jeffrey published an account of another Mesozoic wood presenting the same structural peculiarities as *Cedroxylon transiens*, together with the added abietineous feature of the possession of short or spur shoots, resembling in their anatomical relations those of the living *Pinus*.[5] The latter author, however, differs diametrically in his point of view from Gothan, since he regards *Araucariopitys,* in spite of its numerous abietineous features, as none the less an araucarian conifer and as indicating the derivation of the Araucarinæ from an abietineous ancestry rather than the reverse, as is assumed by Gothan.

---

[1] "The Araucarineæ, Recent and Extinct," *Phil. Trans. Roy. Soc. London,* 1906.

[2] Ginn & Co., Boston, 1907.

[3] "The Megasporophyll of *Saxgothea* and *Microcachrys,*" *Bot. Gazette,* 47, May, 1909.

[4] Gothan, W., "Die Fossilen Hoelzer von Koenig Karls Land," *Kung. Svensk. Vetenskap. Handlingar,* 42, No. 10.

Quite recently Hollick and Jeffrey have published an extensive memoir on the structural remains of the Cretaceous conifers of Staten Island,[6] in which they describe for the first time the anatomical organization of the branches, leaves and cones of a number of well-known Mesozoic conifers hitherto recognized from impressions alone. They reach the conclusion that the external appearance of Mesozoic conifers is in general very misleading as to their real affinities. The supposed Sequoias of the Cretaceous, for example, turn out from the internal examination of all their organs not to belong to the modern genus at all but to be closely related to those araucarian conifers, which are at present limited in their range to the southern hemisphere. The same result is reached in regard to a number of other genera, which have been connected with the living Sequoiineæ, Cupressineæ and even the Podocarpineæ. These authors further conclude that the general structure of Cretaceous conifers of araucarineous affinities is good evidence for the derivation of the Araucarineæ from a stock resembling the Abietineæ and not for the reverse mode of origin, which is universally accepted by those whose conclusions are mainly based on a structural and habital comparison of living conifers with the gymnosperms of the Paleozoic, since the transitional forms are all clearly on the araucarian side.

Sinnott has recently described an araucarian wood, which in the former state of our knowledge would have inevitably been referred to the abietineous genus *Cedroxylon* Kraus.[7] From the study of the ray structure of this fossil wood and from the examination of the tracheids in connection with new criteria recently formulated, this author comes to the conclusion that his wood represents a type of the Araucarineæ, transitional towards the ancestral Abietineæ, which he names *Paracedroxylon,* on account of its general resemblance to the abietineous wood genus *Cedroxylon* Kraus.

---

[5] Jeffrey, E. C., "*Araucariopitys,* A New Genus of Araucarians," *Bot. Gazette,* Dec., 1907.

[6] "Cretaceous Coniferous Remains from Kreischerville, New York," *Mem. New York Bot. Garden,* III, May, 1909.

[7] Sinnott, E. W., "*Paracedroxylon,* A New Type of Araucarian Wood," *Rhodora,* Vol. II, Sept., 1909.

In an important though brief article on the occurrence of the "bars of Sanio" in recent and extinct coniferous woods, Miss Gerry[8] comes to the interesting conclusion that the presence of this structural feature, consisting of transverse bands of cellulose interposed between the radial pits of the tracheids of the wood, is characteristic of all conifers, *except the Araucarineæ.* Her results are of special significance in connection with the conclusions reached by Jeffrey and Hollick, cited above, in regard to the true affinities of the supposed Sequoias, Thuyas, etc., of the Mesozoic. On the basis of the absence of the bars of Sanio in well-preserved woods of supposed Cretaceous Sequoias, etc., she arrives at the result that these are in reality of araucarian affinities, as was inferred by the authors just mentioned, as the consequence of the combined structural study of the branches, leaves and cone-scales of the conifers in question.

The general result of all the investigations cited in the foregoing paragraphs is to show that there existed during the Mesozoic conifers, which were clearly transitional between the abietineous and araucarineous types of the present day. The predominance of the testimony moreover in favor of the Abietineæ rather than the Araucarineæ having been the older coniferous tribe is apparent. Recently Jeffrey has brought forward very definite positive evidence in favor of this view, based on the structure of Mesozoic pines.[9] Known structurally heretofore only as to their wood, the pines of the Cretaceous, which are not without closely allied relatives in the earlier Mesozoic, are here described in relations to the very important features of leaf structure. Among the abietineous remains the most significant because the most archaic genus is *Prepinus* Jeffrey, which has a detailed resemblance in foliar organization to certain Cordaitales of the Paleozoic, as well as the centripetally formed primary wood which is the common possession of the Pteridophyta and the lower gymnosperms. The author was moreover able to trace a complete seriation among various representatives of Cretaceous pines, in leaf organization, from the type presented by *Prepinus,* to that which characterizes contemporary species of *Pinus.* It thus appears that the abietineous line is definitely connected with the

[8] Gerry, Eloise, *Annals of Botany,* Vol. 24, No. 93, Jan., 1910.

[9] Jeffrey, E. C., "On the Structure of the Leaf in Cretaceous Pines," *Annals of Botany,* Vol. 22, No. 86, April, 1908.

Paleozoic gymnosperms, particularly with the Cordaitales, and in this respect has the strongest claim to be considered as the oldest representative of the coniferous stock.

In a recently published article, Jeffrey considers certain abietineous features, such as resin canals of the secondary wood, or the occurrence of marginal ray tracheids, which are found as abnormalities in certain species belonging to the sequoiineous and cupressineous tribes of conifers.[10] He reaches the conclusion that these abnormal abietineous features of the tribes in question are not indications of the derivation of the Abietineæ from them, as has been inferred by Penhallow and others, since recent structural paleobotanical investigations show that the Abietineæ are immeasurably older geologically than the sequoiineous or cupressineous tribes. The conclusion is arrived at that the resin canals or ray tracheids, which sporadically occur in the woods of *Sequoia, Thuya, Sciadopitys, Cunninghamia,* etc., indicate that the Sequoiineæ and Cupressineæ came off from the Abietineæ in the late Mesozoic or early Tertiary, after the latter had developed marginal ray tracheids in their wood rays.

The general result of numerous recent investigations on the anatomy of living and extinct conifers is to show that the two coniferous tribes which have to-day diametrical polar distribution are both very old, reaching back as far as the Paleozoic, that now widely separated geographically and anatomically they once flourished side by side in the northern hemisphere and were connected phylogenetically by a series of transitional forms. The preponderance of evidence moreover seems to vouch for the greater age of the Abietineæ. The more modern and cosmopolitan tribes, the Sequoiineæ, Cupressineæ, Taxineæ, and Podocarpineæ appear further to have been derived from abietineous forebears at a comparatively recent epoch. Even the Podocarpineæ of present characteristic antarctic range, appear from Miss Gerry's interesting investigations, to have come from the general abietineous stock and not from the Araucarineæ, as has been the conclusion of those who have recently investigated the microgametic structures of the araucarians and podocarps, since the latter possess bars of Sanio, which never occur in the Araucarineæ.

E. C. Jeffrey.

Harvard University.

---

[10] "Traumatic Ray-Tracheids in *Cunnighamia sinensis*," *Ann. Bot.*, 22, No. 88, Oct., 1908.

BOOKS **WILLIAM J. GERHARD,**

2209 CALLOWHILL STREET, PHILADELPHIA, PA.,

offers the following at affixed net prices. Extended catalogues of books and pamphlets in all branches of natural history post-free on request :

1.	American Journal of Conchology. 7 vols., partly bound	$25.00
2.	American Journal of Science. Second Series, volumes 1–10. Half roan (3 vols. somewhat waterstained)	10.00
3.	American Mineralogical Journal (Bruce). 1 vol., 1814. New half morocco	10.00
4.	American Monthly Microscopical Journal, vols. 1–20 (1888–1899), of which 14 vols. are half roan	15.00
5.	American Naturalist, vols. 1–6 (1868–72)	9.00
6.	Annals N. Y. Academy of Science, vols. 4–14 (1887–1898). Cloth	22.50
7.	Annuaire du Musée Zoologique de l' Académie des Sciences, St. Petersbourg, vols. 1–7 (1896–1902), lacking one number of vol. 1	10.00
8.	Bulletin American Museum of Natural History, vols. 1–11 (1887–1901)	27.50
9.	De Kay. Zoology of New York—Birds. 4to. Cloth. 141 colored plates	10.00
10.	Gaudry, A. Animaux fossiles et géologie de l'Attique. 2 vols., folio, 1862–67. Half calf, 75 plates and map	35.00
11.	Harlan, R. Medical and physical researches, etc. 1835. Cloth	7.50
12.	Journal and Proceedings Royal Society of New South Wales, vols. 11 (1877) to 23 (1890), except vol. 14. Partly bound in cloth	13.00
13.	King, C. United States Geological Exploration of 40th Parallel. Complete set, 7 vols., quarto, cloth, and two folio atlases	22.50
14.	Microscope (The), vols. 4–11. 8 vols. in four. Half roan	7.50
15.	Morton, S. G. Synopsis of the organic remains of the cretaceous group of the United States. 1834. Half roan. Rare	15.00
16.	Pritchard, A. History of Infusoria, including Désmidiaceae and Diatomaceae. Fourth (last) edition. 1861. Half morocco	8.00
17.	Proceedings Lit. and Philos. Society of Liverpool, vols. 1–34 (except vols. 5, 10, 11, 12, 16, 17, 20, 21), partly bound	16.00
18.	Reports of Explorations and Surveys . . . for a railroad from Miss. River to Pacific Ocean. 13 vols. 4to. Bound	12.00
19.	Smithsonian Miscellaneous Collections, vols. 1–6 (1861–67). Scarce	13.50
20.	Sowerly and Lear. Tortoises, terrapins and turtles drawn from life. Small folio, 1872. Half morocco, 60 finely colored plates	11.00
21.	Transactions American Entomological Society, vols. 1–6. Bound. Scarce	35.00
22.	Transactions Geological Society of Pennsylvania. 1 vol. (1835.) All issued. New half morocco. Rare	15.00
23.	Winter, G. Die Pilze Deutschlands, etc., vols. 1 and 2 (1884–87). Half morocco	7.50

Methods in Plant Histology

By CHARLES J. CHAMBERLAIN,

Second edition, revised and much enlarged; 272 pages, with 88 illustrations, 8vo, cloth; net $2.25, postpaid $2.39

THE first complete manual to be published on the subject of botanical microtechnique. It contains detailed directions for collecting and preparing plant material for microscopic investigation, setting forth the advantages and disadvantages of the different methods.

Will no doubt find a place in every well-regulated library, and will be found very useful by private students.—*Plant World.*

It is an excellent book for the individual worker and for classes in colleges.—*Education.*

A Laboratory Guide in Bacteriology

By PAUL G. HEINEMANN,

158 pages, interleaved, with 37 illustrations, 12mo, cloth; net $1.50, postpaid $1.61

A CLEAR and concise presentation of bacteriological technique, designed principally as a manual for the medical student, but highly useful also as a reference book for the biological teacher and investigator, as well as for practical workers in the fields of medicine and hygiene.

The instruction given is clear and accurate, and the practical exercises are well selected.—*The Lancet* (London).

A book such as this must facilitate very greatly the practical class work, for which it is most excellently adapted. — *American Journal of Medical Sciences.*

The directions are clear and concise, and every stage is described so carefully that it is hard to see how the student can go astray. Physicians who are rusty in bacteriology cannot do better than buy this little book. The book is beautifully printed and bound.—*American Journal of Clinical Medicine.*

Animal Micrology:

Practical Exercises in Microscopical Methods

By MICHAEL F. GUYER,

280 pages, 8vo, cloth; net $1.75, postpaid $1.88

THE title of this book will explain its scope. It is intended as a laboratory manual for textbook use. Its aim is to introduce the student to the technique of microscopic anatomy and embryology, emphasizing details of procedure rather than descriptions of reagents or apparatus. Sufficient account of the theoretical side of microscopy is given to enable the student to get satisfactory results from his microscope.

The directions are simple, explicit, and complete.—*American Journal of Clinical Medicine.*

The medical student will find it very useful as a guide to microscopic work.—*Journal of the American Medical Association.*

This is one of the cleanest works on microscopical technique we have ever seen, and is especially suitable for the beginner. It is full of points, tricks of technique not mentioned in other works, and is one that every student and physician should have.—*Medical Century.*

This valuable book is strong through its rigid exclusion of the trite and the conflicting. It is lucid and helpful, because a man long practiced in practical work has given what he believes the most expeditious and reliable method of obtaining a definite and comprehensive result. — *Medical Notes and Queries.*

A concise, eminently practical, and well-classified treatment.—*Science.*

The expositions of the methods recommended are admirably clear.—*Nature.*

One of the best and most practical works upon microscopic technique with which we are acquainted.—*American Naturalist.*

As a textbook it can hardly be improved. The research worker will find in this book just the information he frequently needs in preparing material with which he is not familiar.—*School Review.*

It does present in very clear form a judicious selection of methods, including an excellent untechnical account of the microscope and its optical principles, adequate for the undergraduate course in histology.— *Journal of Comparative Neurology and Psychology.*

ADDRESS DEPT. 64

Chicago THE UNIVERSITY OF CHICAGO PRESS New York

VOL. XLIV, NO. 521 MAY, 1910

THE
AMERICAN
NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with
Special Reference to the Factors of Evolution

CONTENTS

Page
I. A Review of Some Recent Criticisms of the Restorations of Sauropod Dinasaurs. Dr. J. W. HOLLAND . . . 259
II. Anatomical Characters in the Evolution of Pinus. IRVING W. BAILEY . 284
III. Facts about the "Lobster Pearl." Professor FRANCIS H. HERRICK . . 294
IV. Shorter Articles and Discussion:
An Eighteenth Century Microscope: Professor BASHFORD DEAN. Stomatolepas, a Barnacle Commensal in the Throat of the Loggerhead Turtle. HENRY A. PILSBRY. The Age of Speed Sires: CASPER L. REDFIELD 302
V. Notes and Literature:
Biometrics—Recent Quantitative Studies in Variation in Social Insects: Dr. RAYMOND PEARL. *Experimental Zoology*—The Effects of Extirpation and of Transplantation of the Reproductive Organs in Insects: E. N. BROWNE. Wheeler on Ants: Professor G. H. PARKER 308

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS
Lancaster, Pa. Garrison, N. Y.
NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

TO ORNITHOLOGISTS
AND MUSEUMS

W. F. H. ROSENBERG
Importer of Exotic Zoological Specimens
57 Haverstock Hill, N.W., England

Begs to announce the publication of a new Price List (No. 11) of **Bird Skins**. This catalogue contains over 5,000 species, and is the largest and most complete price list of birds ever published. It is arranged in systematic order, based on the classification of the British Museum "Catalogue of Birds," with authors' names, indications of localities, and an index to families. It will be sent gratis and post free on application, as will the following lists:
No. 7, Mammals; No. 8, Birds' Eggs;
No. 9, Reptiles, Amphibia, and Fishes.

Largest stock in the world of specimens in all branches of Zoology.

Specimens sent on approval.

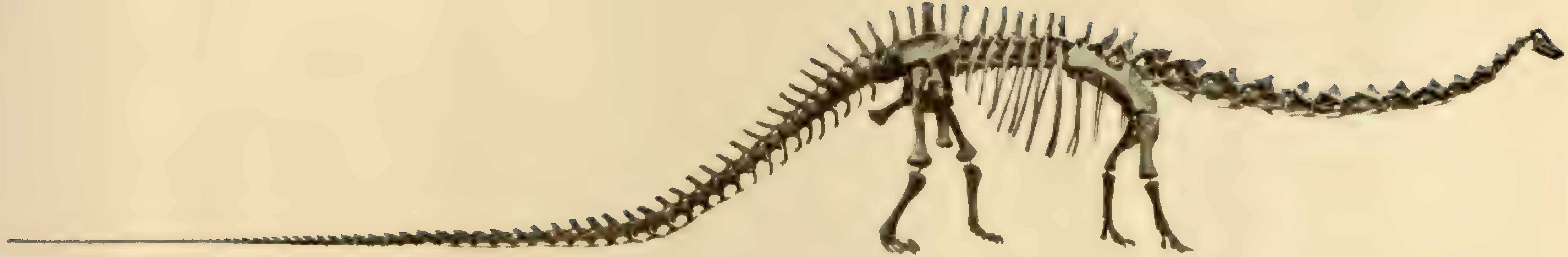
Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

Henry Holt & Company
34 West 33d St., New York
378 Wabash Ave., Chicago

Microscopes and Accessories
Hand Cameras of Highest Quality
Binoculars, Prism and Galilean
the best obtainable for Nature Study
Scientific Instruments
Laboratory Apparatus
Max Meyer 18 West 27th St. New York
"Quality, Prices, Service Right."



THE SKELETON OF DIPLODOCUS CARNEGIEI, MOUNTED IN THE CARNEGIE MUSEUM, PITTSBURGH

THE LENGTH FROM THE TIP OF THE NOSE TO THE END OF THE TAIL OVER CURVES IS 84½ FEET; THE HEIGHT AT THE HIPS IS ABOUT 14 FEET. REPLICAS THUS MOUNTED ARE LOCATED IN BERLIN, PARIS, VIENNA AND BOLOGNA

THE
AMERICAN NATURALIST

VOL. XLIV *May, 1910* No. 521

A REVIEW OF SOME RECENT CRITICISMS OF THE RESTORATIONS OF SAUROPOD DINOSAURS EXISTING IN THE MUSEUMS OF THE UNITED STATES, WITH SPECIAL REFERENCE TO THAT OF DIPLODOCUS CARNEGIEI IN THE CARNEGIE MUSEUM[1]

DR. W. J. HOLLAND

CARNEGIE MUSEUM

ALL paleontologists are familiar with the figure of *Brontosaurus excelsus* Marsh, which was originally published in the *American Journal of Science* in August, 1883, and republished with modifications in the same periodical in 1895. This figure has since been frequently reproduced in text-books. Paleontologists are also familiar with the restoration of the skeleton of *Diplodocus carnegiei* Hatcher, which originally appeared in the *Memoirs of the Carnegie Museum*, and is reproduced in the second volume of the English translation of Zittel's "Text-book of Paleontology," by C. R. Eastman. Since the time when Mr. Hatcher made this restoration the acquisition of new material has thrown much light upon the subject, and certain changes in the pose have been suggested, which are reflected in the accompanying illustration (Plate I), which is taken from a photograph of the splendid specimen in the Carnegie Museum, replicas of which have been generously presented by Mr. Andrew Carnegie to a number of the leading museums of Europe.

---

[1] The substance of this paper was communicated to the Annual Meeting of the Paleontological Section of the Geological Society of America on December 30, 1909. The paper at that time was freely illustrated by means of the stereopticon, and a number of the pictures and diagrams then used are herewith reproduced.

In *The Field* (London) of August 26, 1905, Mr. F. W. Frohawk, a well-known English illustrator, published a note, in which he said, among other things:

> The visitor to the Reptile Gallery of the Natural History Museum can not fail to be struck by the extraordinary pose of the gigantic skeleton. . . . It would be interesting to know the reason for mounting the specimen so high on its legs, like some huge pachyderm. As it is a gigantic lizard, why should it not be represented in the attitude usually assumed by such animals? . . . Doubtless there is some good reason for mounting it in such an attitude; if so, information on the subject would be welcome.

No reply was given to this query, except incidentally by Professor (now Sir) E. Ray Lankester, who said in a newspaper interview that "the laterally compressed form of the body, according to the opinion of American students, precludes the idea that the animal could have crawled upon its belly."

Shortly after the restored skeleton of *Brontosaurus excelsus*, which is one of the ornaments of the American Museum of Natural History, had been erected, Messrs. Otto and Charles Falkenbach, assistants in the paleontological laboratory of that museum, made a model, in which they attempted to show the *Brontosaurus* in a crawling attitude. I am indebted to Dr. W. D. Matthew for an illustration of this model, which is herewith reproduced (Fig. 1). This model was discussed at the meeting of the American Society of Vertebrate Paleon-

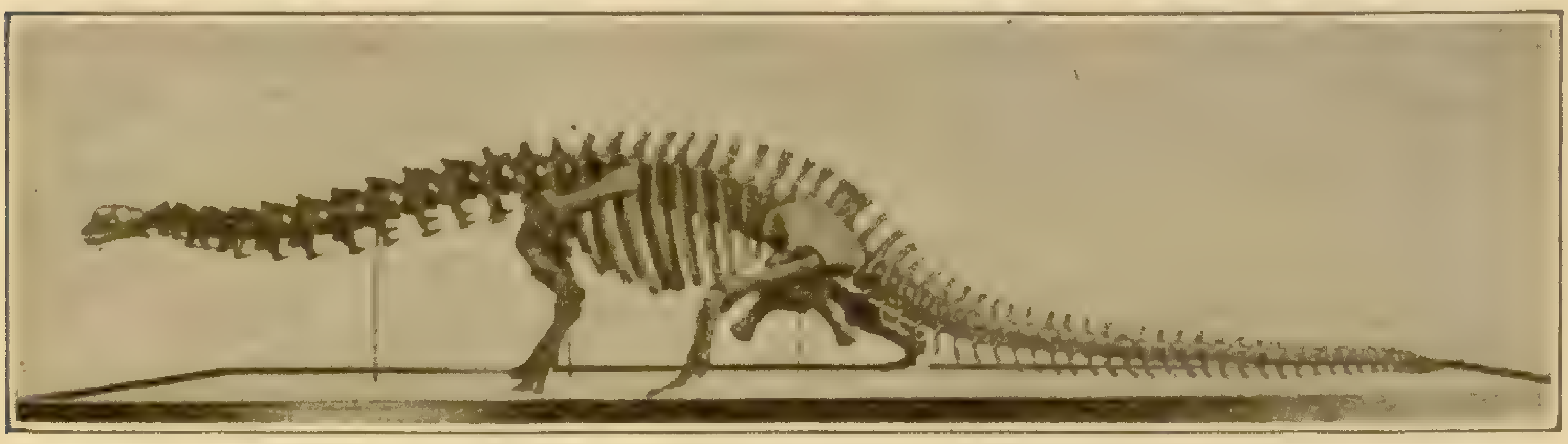


FIG. 1. Small Model of Skeleton of *Brontosaurus excelsus* Marsh, made by Messrs. O. and C. Falkenbach.

tologists held at the American Museum of Natural History in 1906, and by common consent was judged for many reasons to represent the impossible.

In October, 1908, there appeared in Vol. XLII of THE AMERICAN NATURALIST an article from the pen of Dr. Oliver P. Hay, "On the Habits and Pose of the Sauropod Dinosaurs, especially of Diplodocus." Dr. Hay maintains that in assembling the fossil remains of these animals they should have been given a crocodilian attitude. At the conclusion of his article he sums up his views in the following words:

> It seems to the writer that our museums which are engaged in making mounts and restorations of the great sauropoda have missed an opportunity to construct some striking presentations of these reptiles that would be truer to nature. The body placed in a crocodile-like attitude would be little, if any, less imposing than when erect; while the long neck, as flexible as that of an ostrich, might be placed in a variety of graceful positions.

This article of Dr. Hay was followed by a paper from the pen of Dr. Gustav Tornier, who, taking his cue from Dr. Hay, has tried to show that American paleontologists have totally erred in their conception of the structure of the sauropod dinosaurs, and has given his views as to the manner in which the bones of the *Diplodocus* should have been assembled. His paper is embellished by a number of cuts. Professor Tornier's paper was followed in the popular scientific journal *Aus der Natur* by an article from the pen of Dr. Richard Sternfeld, in which he endorses the views of Tornier and endeavors to hold American paleontologists up to ridicule, asserting that they have "literally, from head to foot, misconstructed the *Diplodocus,* and probably also its near allies." Sternfeld enlarges upon Tornier's views and gives some illustrations of his own.

In the manner of a man who has made a wonderful discovery, Tornier announces at the outset of his paper that *Diplodocus* is a genuine reptile—"ein echtes Reptil." No student of the sauropoda has ever doubted this. But having predicated the genuinely reptilian character of the animal, Tornier proceeds thereafter to speak of the *Diplodocus* as a lacertilian—"ein Eidechse." There are reptiles and reptiles. Having assured himself of the truly reptilian character of the animal, it was a bold step for him immediately to transfer the creature from the order Dinosauria, and evidently with the skeleton of a *Varanus* and a *Chameleon* before him, to proceed with the help of a pencil, the powerful tool of the closet-naturalist, to reconstruct the skeleton upon the study of which two generations of American paleontologists have expended considerable time and labor, and squeeze the animal into the form which his brilliantly illuminated imagination suggested. The fact that the dinosauria differ radically from existing reptiles in a multitude of important structural points seems not to have greatly impressed itself upon the mind of this astute critic. He intimates that the pelvis of *Diplodocus* is distinctly lacertilian. He states that the great trochanter of the femur, which he does not designate as such, articulated with the ischial peduncle, and takes care to show the point of union by means of a lettered diagram, which I herewith reproduce (Fig. 2). He takes pains to show that (*e*) the great trochanter, articulates with (*c*) the

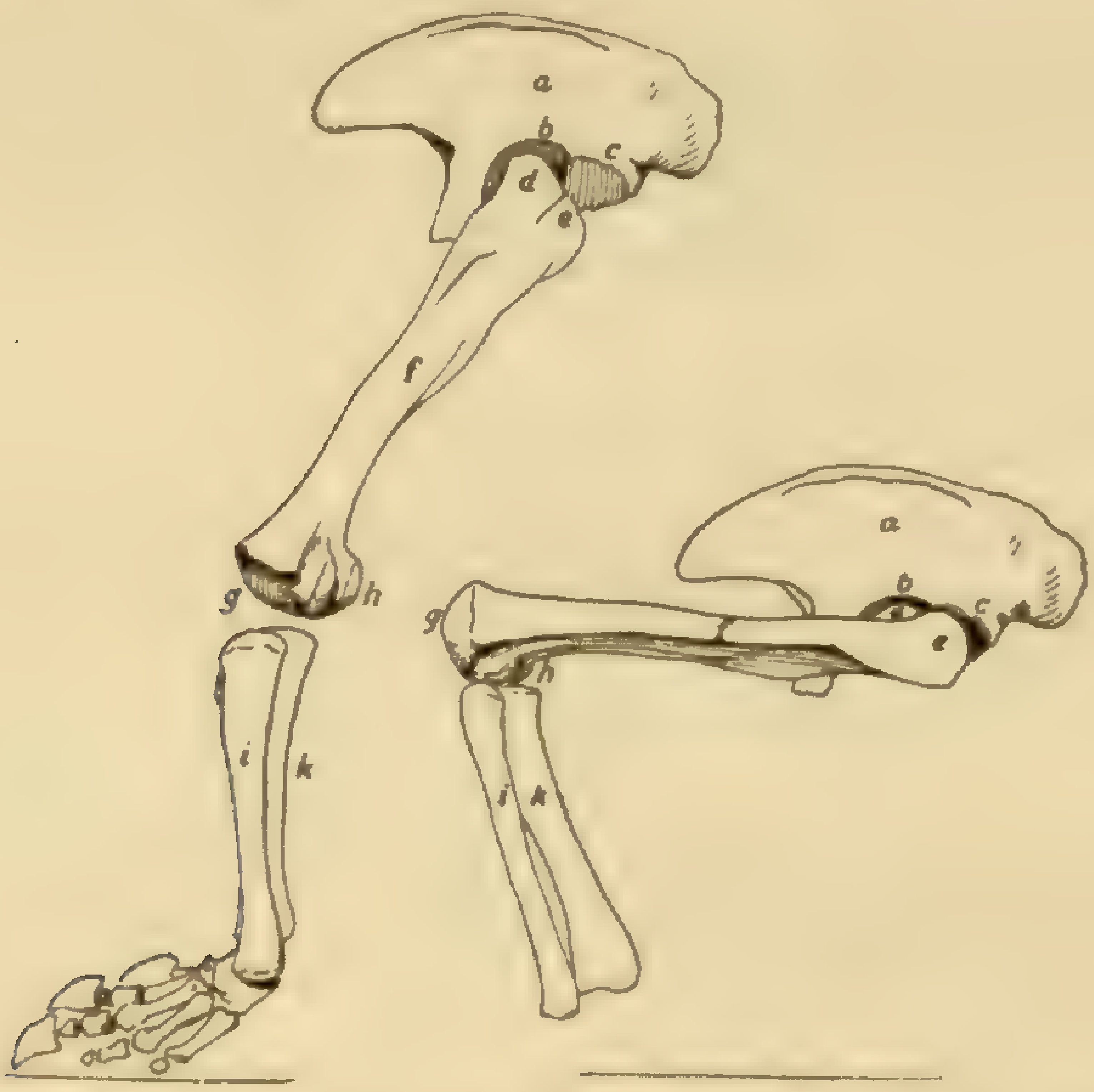


FIG. 2. Reproduction of figure given by Dr. Tornier in which he endeavors at the left to show the hind limb of *Diplodocus* as mounted, and at the right the position which he claims the limb should have.

ischial peduncle. It may be said in passing that Dr. Tornier takes very great liberties with the outlines of the bones. His drawing is very far from accurate. Unfortunately actual experiment shows, *first,* that it is impossible except by smashing the ilium or breaking the femur to jam the head of the latter into the position demanded for it by the learned professor; but, *second,* this is the only time, it is believed, in the history of anatomical science that any one has discovered that the great trochanter of the femur ought to be and is by nature intended to be articulated with the ischial peduncle of the ilium, thus locking the femur into a position utterly precluding all motion whatsoever.

The next step taken by this wonder-working comparative anatomist was to dislocate the knee-joint. This he proceeds to do in a most nonchalant manner, and leaves the articulating end of the femur peering forth into space (see Fig. 2, *g*), while the tibia and the fibula are made to articulate with the posterior edges of the interior and exterior condyles of the femur. Having adopted this change, he succeeds in so lowering the hind quarters of the *Diplodocus* that they must rest upon the anterior extremity of the pubic bones, which, with the fragile ends of the ribs, not much greater in size than those of an ox, have thrown upon them the entire weight of the carcass. To obviate the inconveniences of this pose the lead pencil is again brought into requisition and the anterior vertebræ are hoisted into the air and propped up upon the scapulæ, the dorsal ends of which have been glued by a hypothetical suprascapula to the lateral processes of the last cervical vertebræ (see Fig. 3). This transference of the scapula to the Tornerian position is done in order to give, as the author says, an opportunity to so place the scapula that horizontal motion backward and forward may be allowed to the humerus, which he takes pains to inform us is strikingly like that of a *Varanus.* Upon the latter point it is quite possible to differ from the learned critic.

The anterior portion of the trunk having been thus elevated, the fore legs are again dislocated at the juncture of the humerus with the radius and ulna and stuffed underneath the skeleton, while the great neck is thrown upward in the form of a reversed letter "S," the Hogarthian lines of which no doubt suggested themselves to the learned reconstructionist as possessing soulful grace. A reproduction of the skeletal monstrosity perpetrated by Tornier is here given (Fig. 3). As a contribution to the literature of caricature the success achieved is remarkable. It reminds us somewhat of those creations carved in wood emanating from Nuremberg, which were the delight of our childhood, and which came to us stuffed in boxes labeled "Noah's Ark," and stamped "Made in Germany."

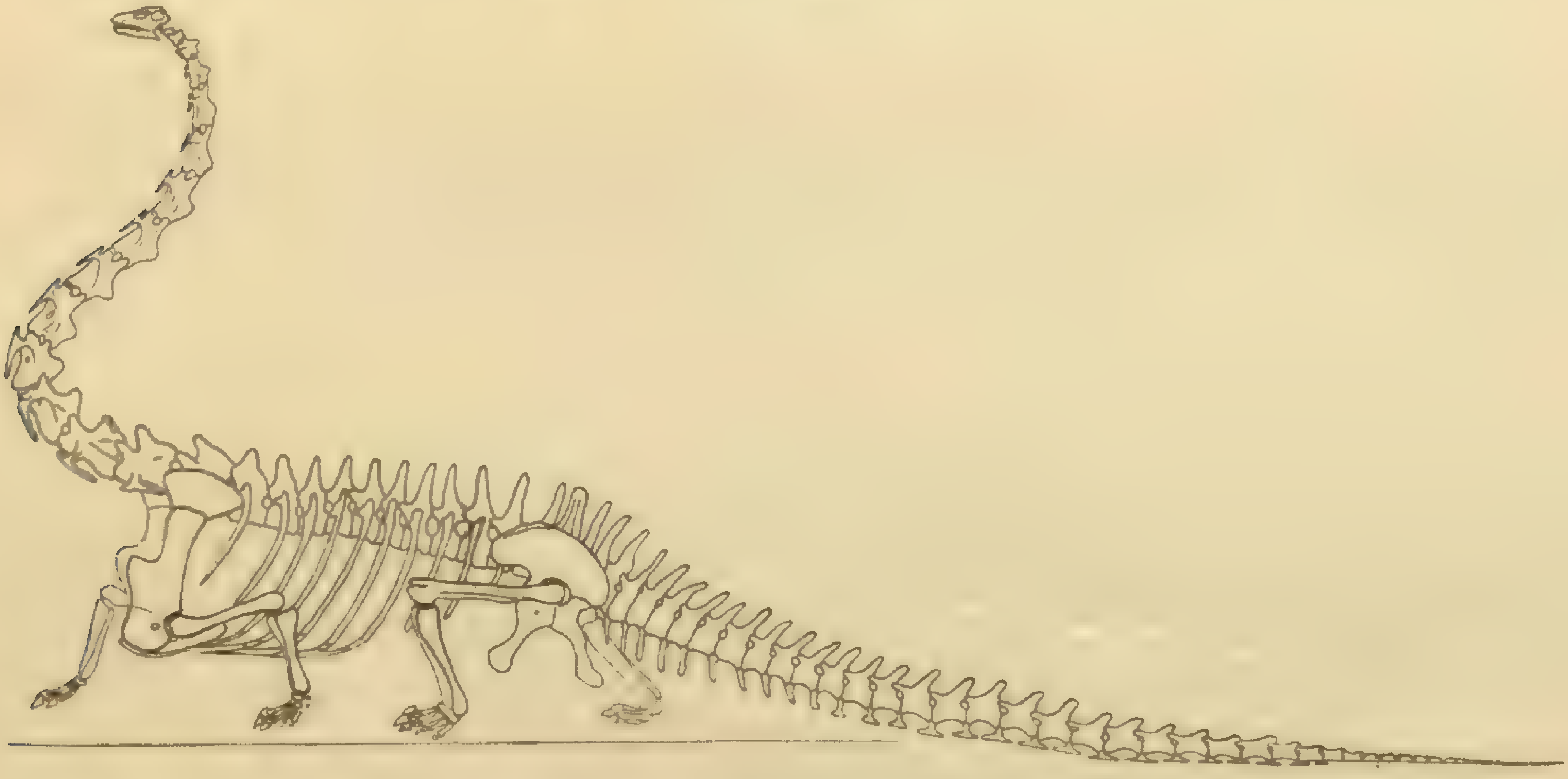


FIG. 3. The skeleton of *Diplodocus* mounted according to Tornier in the correct position "Richtige Stellung."

I should prefer to end my communication at this point, commending the perusal of the articles by Hay, Tornier, and Sternfeld to the attention of those of you who are familiar with the osteology of the sauropoda as amusing illustrations of the manner in which it is possible for gentlemen possessing entirely inadequate acquaintance with a subject to "darken counsel by words without knowledge."

Inasmuch, however, as Professor Tornier's opinions and his misleading diagrams and figures have been given some currency in journals intended to popularize science, it seems to the speaker that the present is a suitable occasion in which not merely to demonstrate the utterly absurd character of the opinions of Hay, Tornier, and Sternfeld, but also to bring out into clearer light the reasons why American paleontologists, and for that matter the leading paleontologists of Europe also, have concurred in regarding the sauropod dinosaurs as having possessed the power to assume the position which has hitherto been given them. At the risk, therefore, of occupying some of your precious time I wish to take up the subject a little more thoroughly and by the help of a series of illustrations to make my meaning clear.

I shall begin with the structure of the pelvis in the sauropod dinosaurs. I herewith give illustrations (Fig. 4) taken from the specimens in the Carnegie Museum of the pelves of *Brontosaurus*, *Diplodocus*, and *Haplocanthosaurus*, the last closely allied to *Cetiosaurus* of Owen.

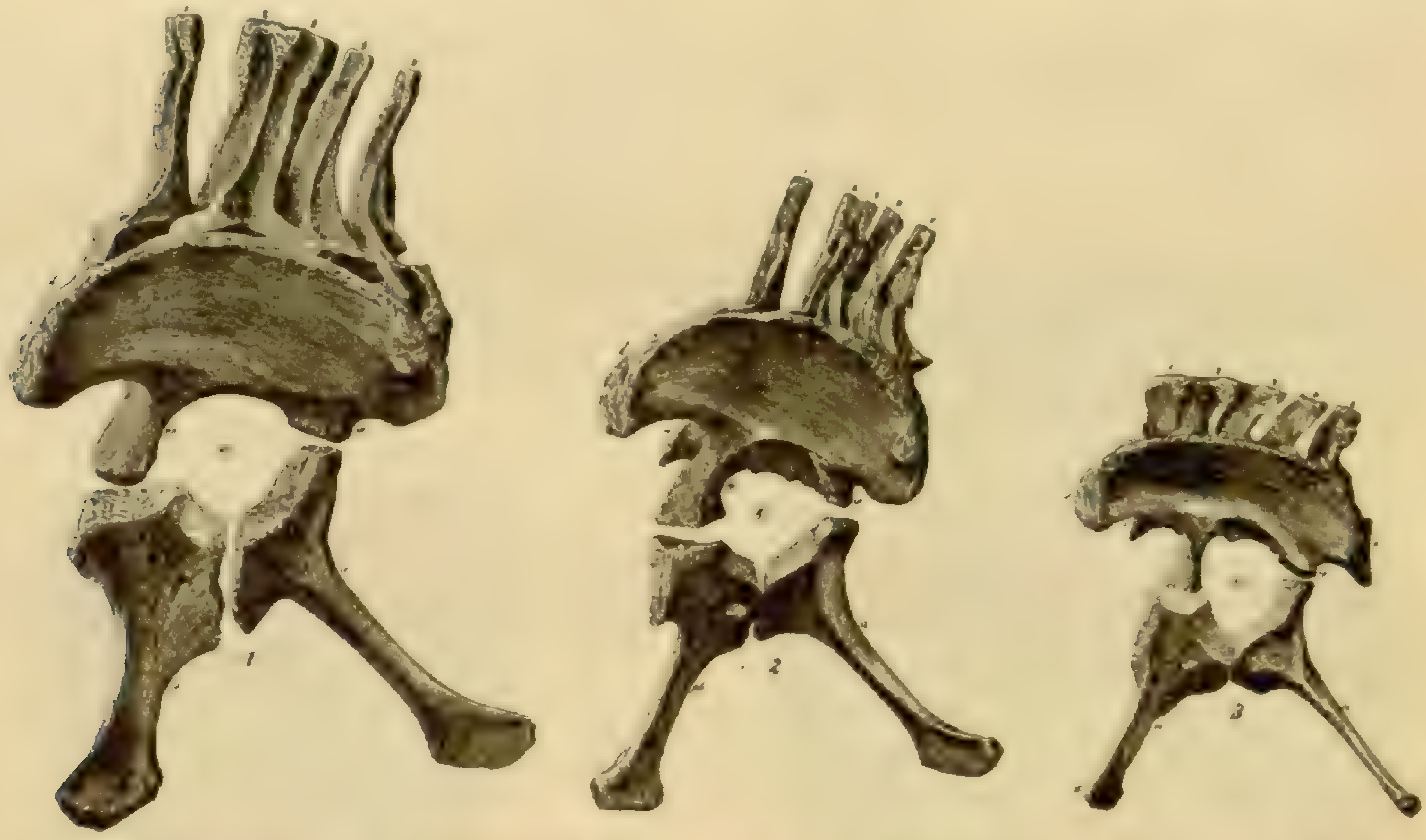


FIG. 4. 1, pelvis of *Brontosaurus;* 2, pelvis of *Diplodocus;* 3, pelvis of *Haplocanthosaurus.* From specimens in the Carnegie Museum.

Any one who has a merely rudimentary knowledge of the pelves of the dinosauria in general knows that they are distinctly ornithic in type, and not lacertilian, nor crocodilian, Professor Tornier to the contrary notwithstanding. Seeing is believing, and I also give illustrations of the pelvis of a crocodile, of *Varanus*, of *Iguana*, and of *Uromastrix* (Figs. 5–8). Compare these for a moment with the pelves of the huge sauropod reptiles and you see immediately that there is an enormous difference in general, and in countless details, which it is not worth while to consume your time in describing.

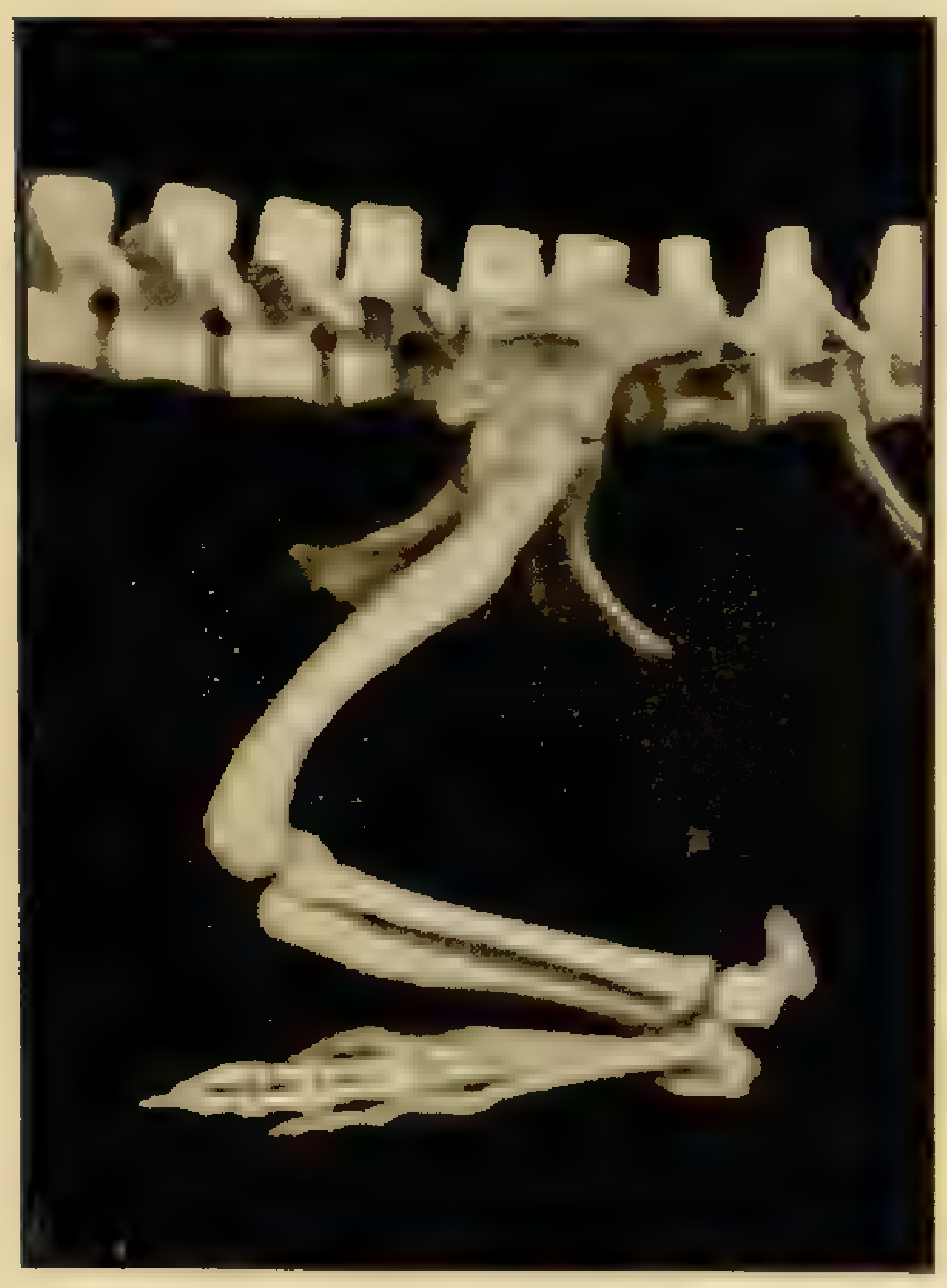


Fig. 5. Pelvis and hind limb of crocodile.

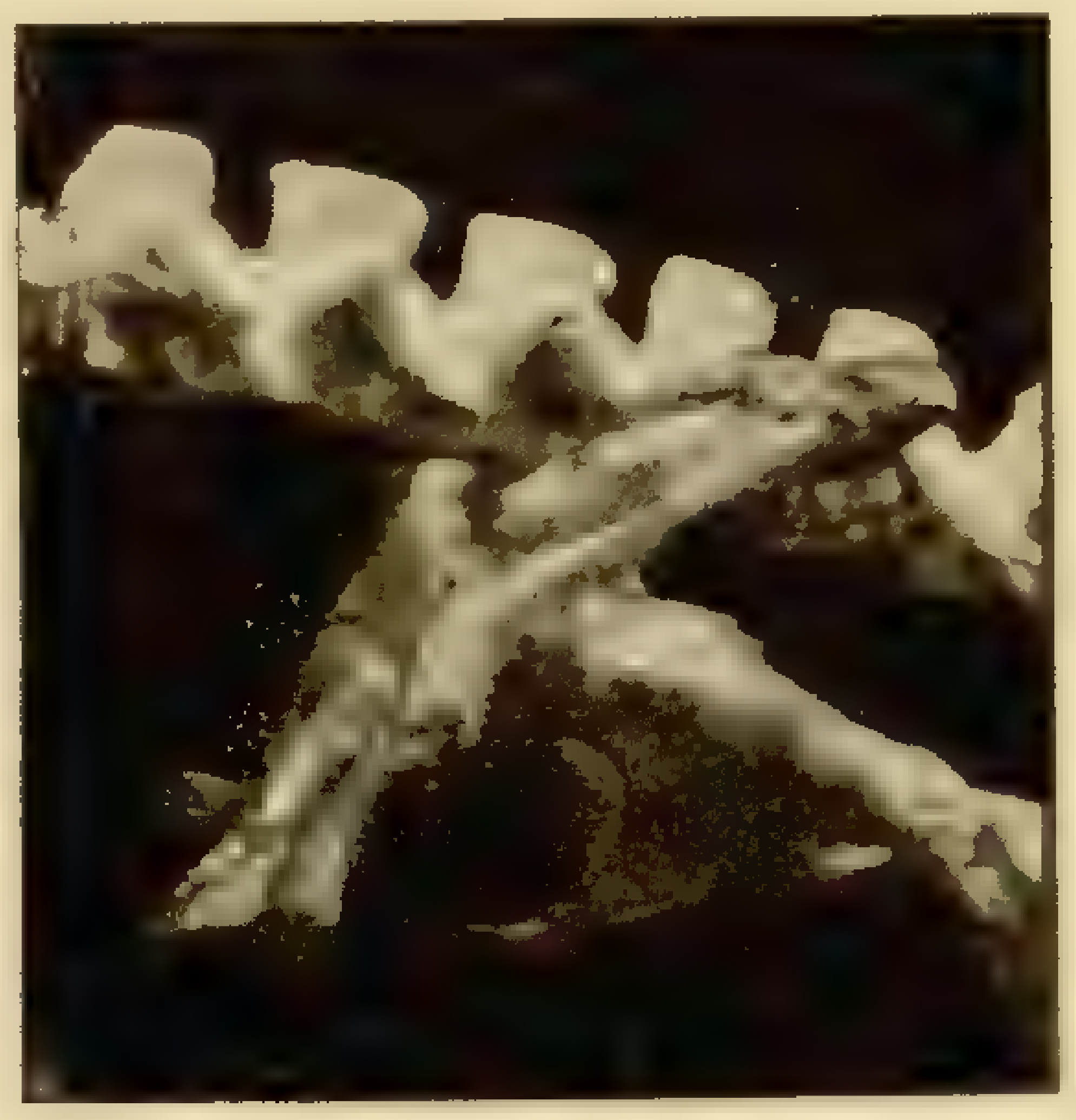


Fig. 6. Pelvis of *Varanus*.

Taking up now the articulation of the femur with the acetabulum of the pelvis, we discover in the first place that the head of the femur in the lacertilia differs remarkably from the head of the femur in the sauropoda.

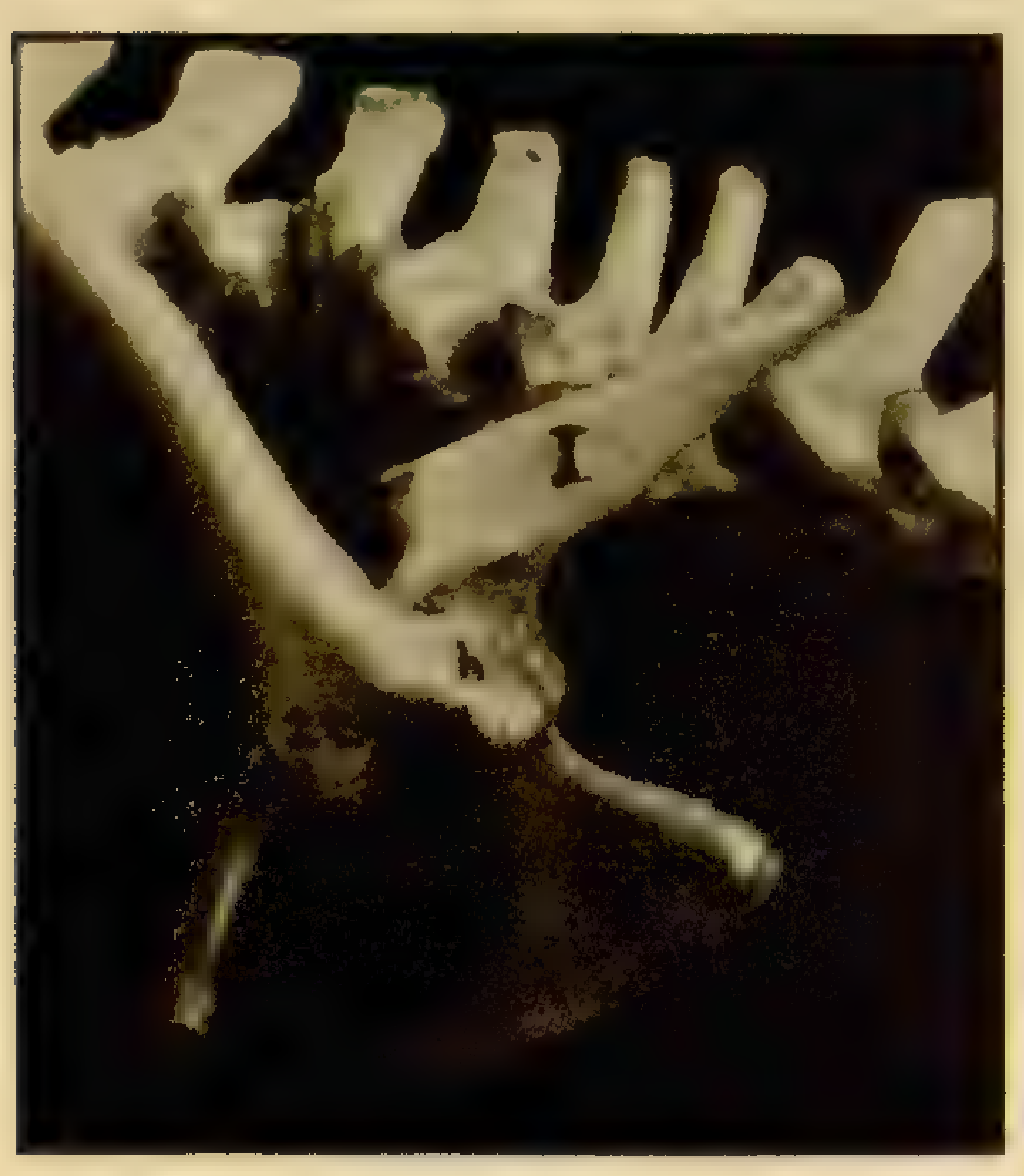


Fig. 7. Pelvis of *Iguana*. I, Ilium; *h*, Head of femur; 2*t*, Second trochanter.

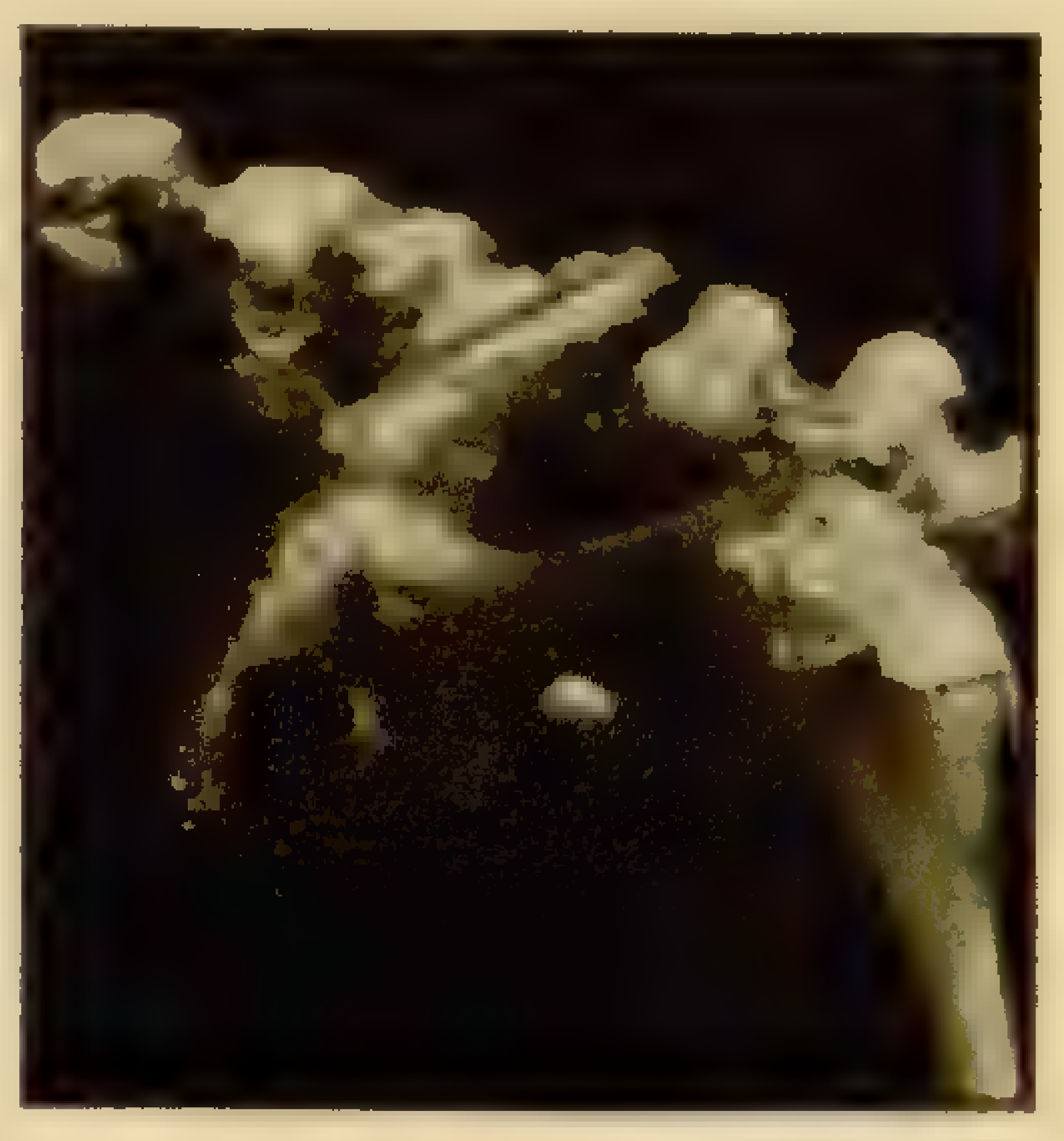


Fig. 8. Pelvis of *Uromastrix*.

In the lacertilia the greater trochanter is reduced in size and in some genera is practically obsolete; when present and articulated it looks backward, downward, inward. On the other hand, the second trochanter in the recent lacertilia is enormously developed, looking downward, forward, and outward (see Fig. 7). In the sauropoda, as in the ratite birds, the second trochanter is obsolescent or wholly obsolete. The illustrations already given may help to make my meaning clear. In this connection it is well to study the head of the femur and the structure of the pelvis in the struthious birds. The analogy between these and the dinosauria has often been pointed out. The facts to which I have called your attention have great anatomical significance. A comparison of the head of the femur of the crawling reptiles of to-day with the femur of the sauropoda shows at a glance that in the latter the proximal end of the femur is more like that of birds than of recent lizards. It was, as we all know, in consequence of the recognized similarity of the pelvic girdle and the head of the femur to the corresponding structures in the ratite birds that Owen, Marsh and all other competent students have assigned the femur the position which has almost uniformly been given to it in restorations of the sauropoda, as well as of other dinosaurs.

But let us for the sake of experiment give the femur the same relative position which it has in the lacertilia, in which the second trochanter plays so great a part. To do this it is necessary to rotate the head of the femur in such a way that the great trochanter will point downward and backward. The accompanying diagrammatic illustration shows the femur of the *Diplodocus* adapted to the acetabulum after the analogy of *Varanus* and *Iguana* (Fig. 9). Of what earthly use the hind limb of the *Diplodocus* could have been to him in such a position I leave you to determine for yourselves. It has been suggested that kindly nature, to meet the requirements of the case, must have channeled the surface of the earth and provided the *Diplodocus* and its allies with troughs in which they kept their bodies while the feet were employed for purposes of locomotion along the banks. The *Diplodocus* must have moved in a groove or a rut. This

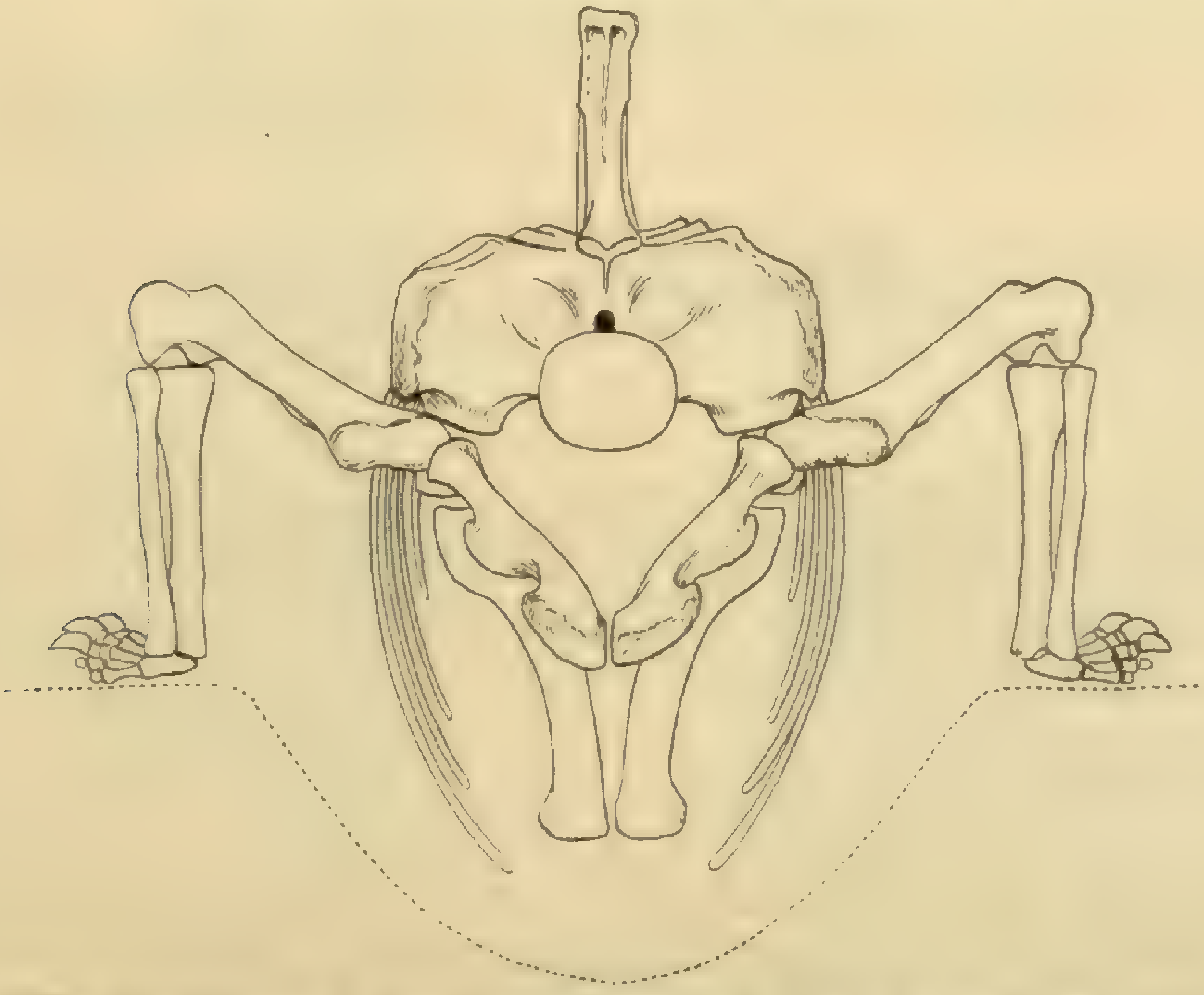


FIG. 9. The hind limbs of *Diplodocus* arranged after the analogy of the recent lacertilia.

might perhaps account for his early extinction. It is physically and mentally bad to "get into a rut."

Assuming that the articulation of the femur after all was not as it is in the lacertilia, and accepting, merely for the sake of argument, the pose of Professor Tornier, who, though contending that the creature was a lacertilian—"ein Eidechse"—nevertheless, constrained by obvious difficulties, in his drawings does not give the femur the characteristically lacertilian pose, I have taken pains to place the bones of the replica of the *Diplodocus* now in course of preparation for the Imperial Academy at St. Petersburg as nearly as is possible in the position which Professor Tornier demands that they should have. I have accepted Tornier's "richtige Stellung" for the time being, and have collocated the bones in the position which he demands for them, and I have the pleasure herewith of submitting to you photographs of the bones thus located (Figs. 10 and 11). In the first place you will observe that it is beyond possibility, when locating the bones in this manner, to bring about anything like a plausible position of the head of the femur in the acetabulum. The ridiculous articulation of the great trochanter with the ischial peduncle demanded by Professor Tornier, who seems to have mistaken the ischial peduncle for an anti-trochanter, has already been alluded to. Of course we could not accomplish such an articulation, but we have come as near to it as the bones will allow. Placed as nearly as is possible in the situation in which Professor Tornier demands that the bones shall be put, the head of the femur stands in no relation whatever to the articulating surfaces of those portions of the pubis and the ischium (*a.p* and *a.i*) which enter into the composition of the acetabulum. The lower surface of the head of the femur is left out of all relation to these obviously articulating surfaces at a remove from them of at least six inches. Furthermore, in swinging the

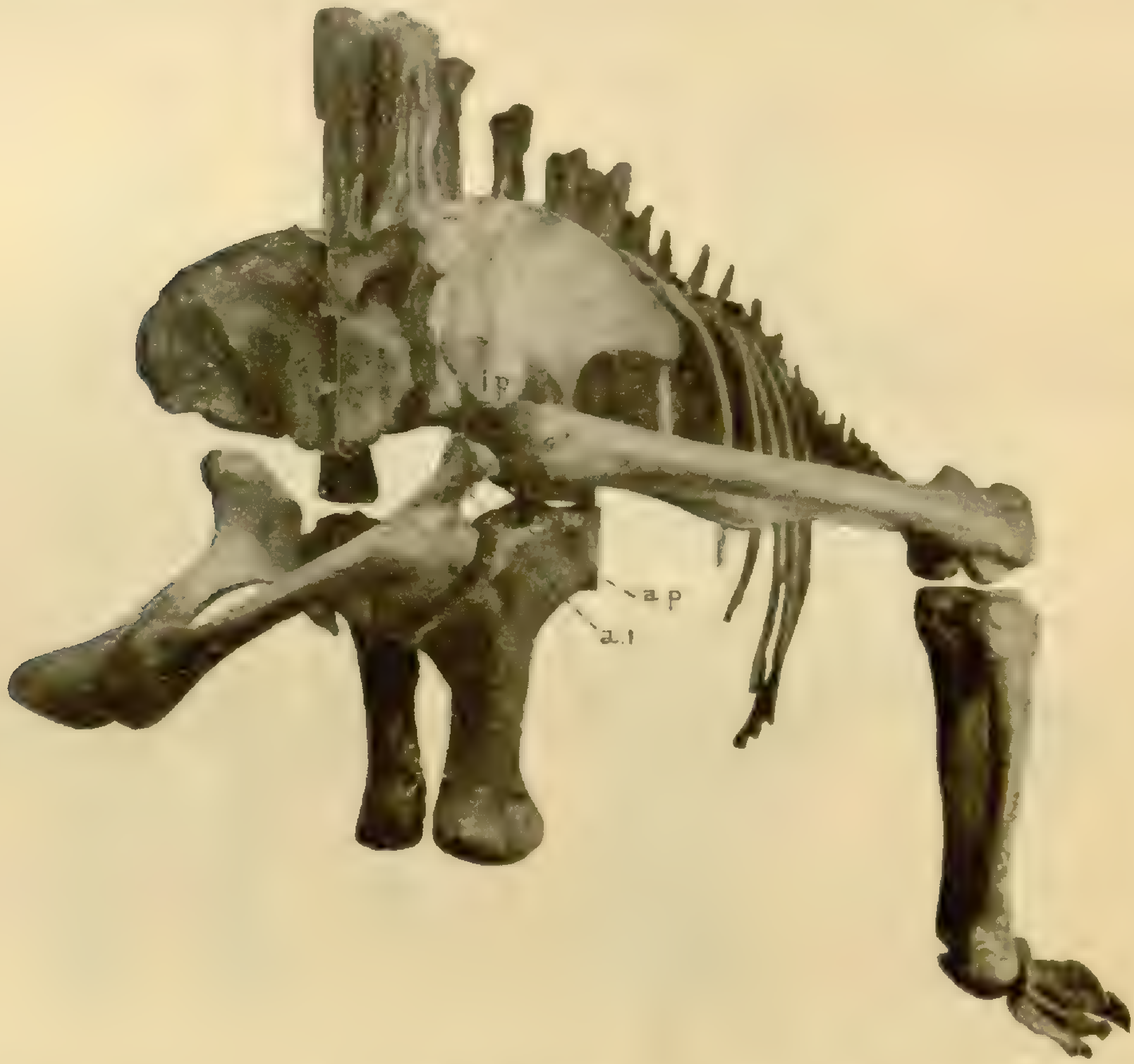


FIG. 10. View from behind of pelvis and femur of *Diplodocus* mounted according to the Tornierian prescription. *i.p*, Ischial peduncle; *g.t*, great trochanter; *a.p*, acetabular surface of pubis; *a.i*, acetabular face of ischium.

bones into the acetabulum in such a way as to throw the distal end outward, the head of the femur necessarily enters and penetrates the opening of the acetabulum, invading the pelvic cavity and occluding the same. But this is not the worst. The distal end of the femur is left, as Tornier's figures themselves show, protruding into space without any surface whatever with which to articulate. I am fully aware that in the lacertilia the joint made by the femur with the tibia and fibula, especially in young individuals, is provided to a high degree with cartilaginous connections, and the ends of the bones are covered

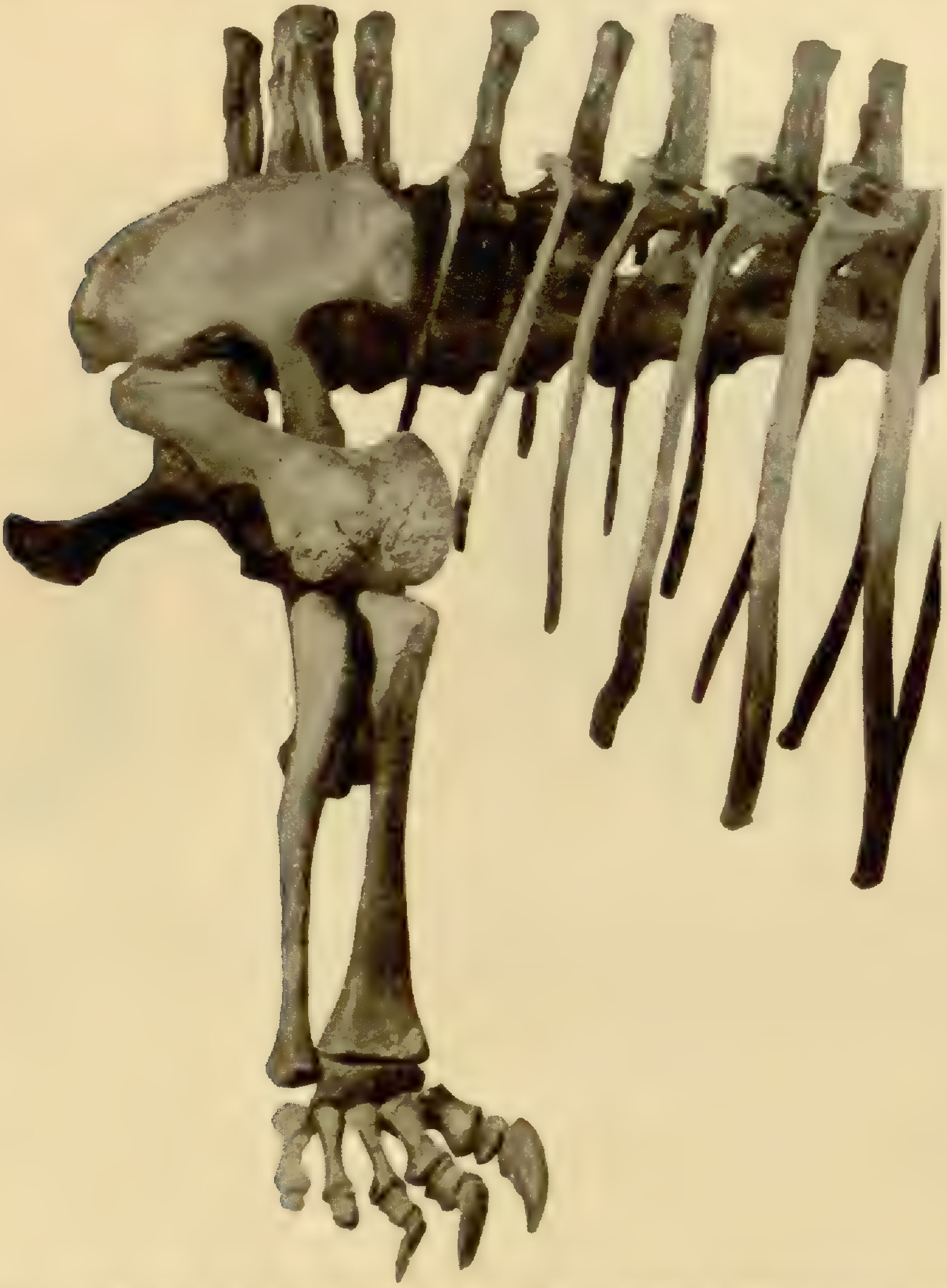


FIG. 11. View from side and front of femur and pelvis of *Diplodocus* mounted after the Tornierian prescription.

with great cartilaginous epiphyses, which in the bones of the fossil animals we are considering have not been petrified and preserved, but making all allowance for the existence of these cartilaginous masses at the points indicated, it is impossible to conceive that the broad expanded heads of the tibia and fibula should merely come in contact with the internal and external condyles of the femur at two small points, in each case not larger than a sixpence. The pose given to these bones by Dr. Tornier represents nothing else than the complete dislocation of the femur from the tibia and fibula.

Dr. Tornier labors long with the scapula and the humerus. As I have already stated, he claims that the humerus of *Diplodocus* is startlingly—"verblüffend"—like that of *Varanus*. It is wonderful what a man can see who has determined to see things! If you will simply take the trouble to compare the humerus of the sauropod dinosaurs with that of a *Varanus* I think you will be able without opening your eyes very widely to discover a number of startling differences. In addition to falling into error as to the startling likeness existing between the humerus in the sauropoda and the lacertilia, he makes a multitude of grossly inaccurate and misleading statements in uttering the special plea which he makes for his theory. It would be wearisome to recall them. One of the more noticeable misstatements is made when he declares that the coracoid bone belongs on the lower side of the belly—"Bauchunterseite." The coracoid, as we all know, is a sternal element and has nothing whatever to do with the "Bauch," or belly. He

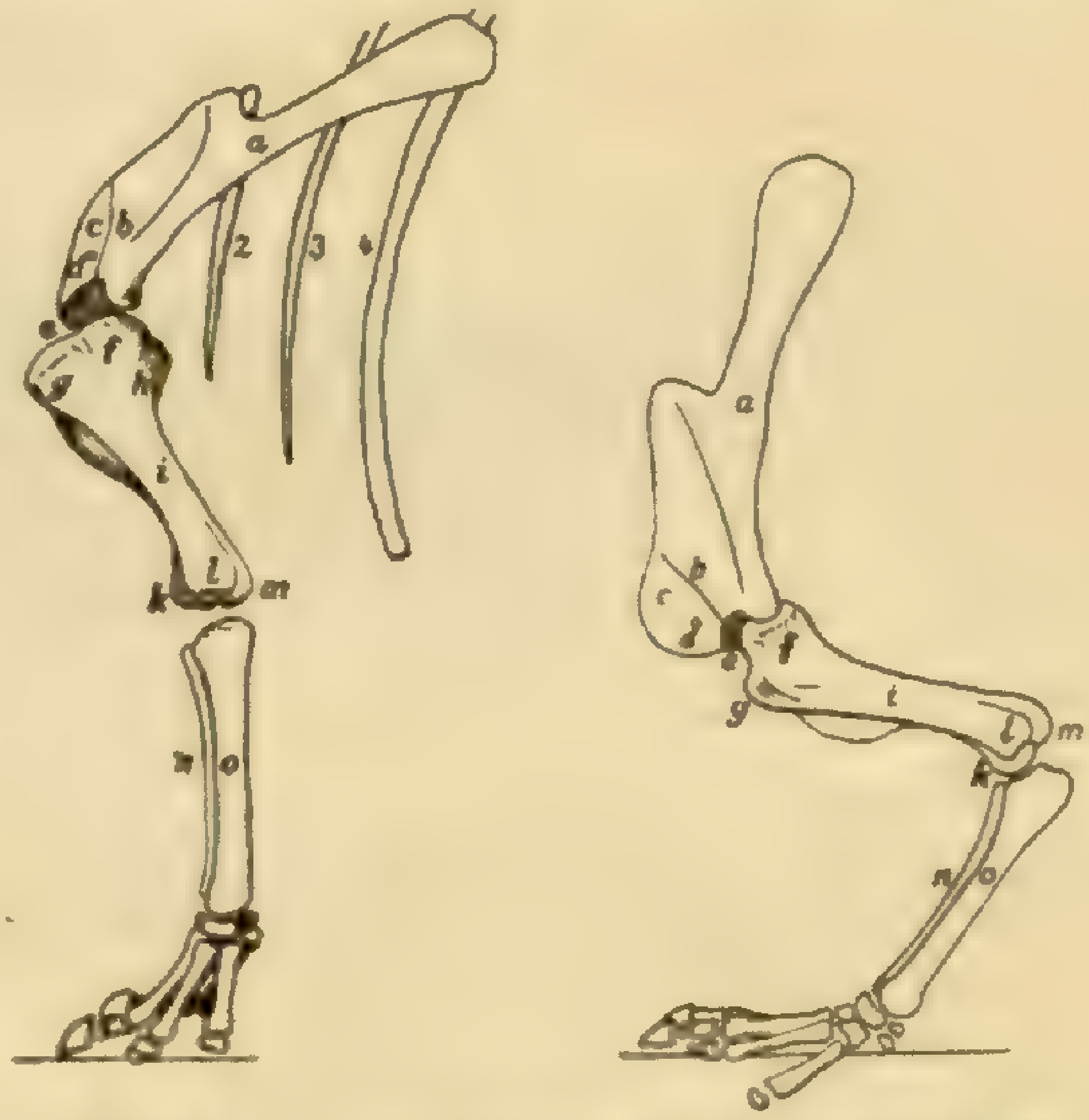


FIG. 12. Reproduction of figures given by Tornier showing the restoration of scapula and fore limb of *Diplodocus* as he alleges it to be (left figure), and as he claims it should be (right figure).

ignores the fact that the superior surfaces of the anterior ribs and the lateral processes of the anterior dorsal vertebræ unite to form a surface evidently adapted to the end of providing a field over which the long dorsal blade of the scapula can play. He demands for the scapula a vertical position so as to give to the humerus an opportunity, as he says, to move in a horizontal plane backward and forward. He states that a vertical position of the scapula is universal among recent reptilia, which is not the case. It is true of the lacertilia, but it is not true of the crocodilia. I herewith give a reproduction of a drawing copied from Blainville of a crocodilian skeleton, and another copied from Brühl (Fig. 13), both of which show that the scapula in the crocodile has a position in the articulated skeleton similar to that which it has in the mammalia. But lest some one may say that the artists were mistaken, I am able through the kindness of Dr. Geo. C. Johnston, of Pittsburgh, the well-known radiographer, to exhibit a number of X-ray photographs showing the scapula in position in the common American alligator[2] (Fig. 14). These photographs show the entire accuracy of the drawings of Blainville and Brühl. And I am prepared to further verify the drawings by an example of an

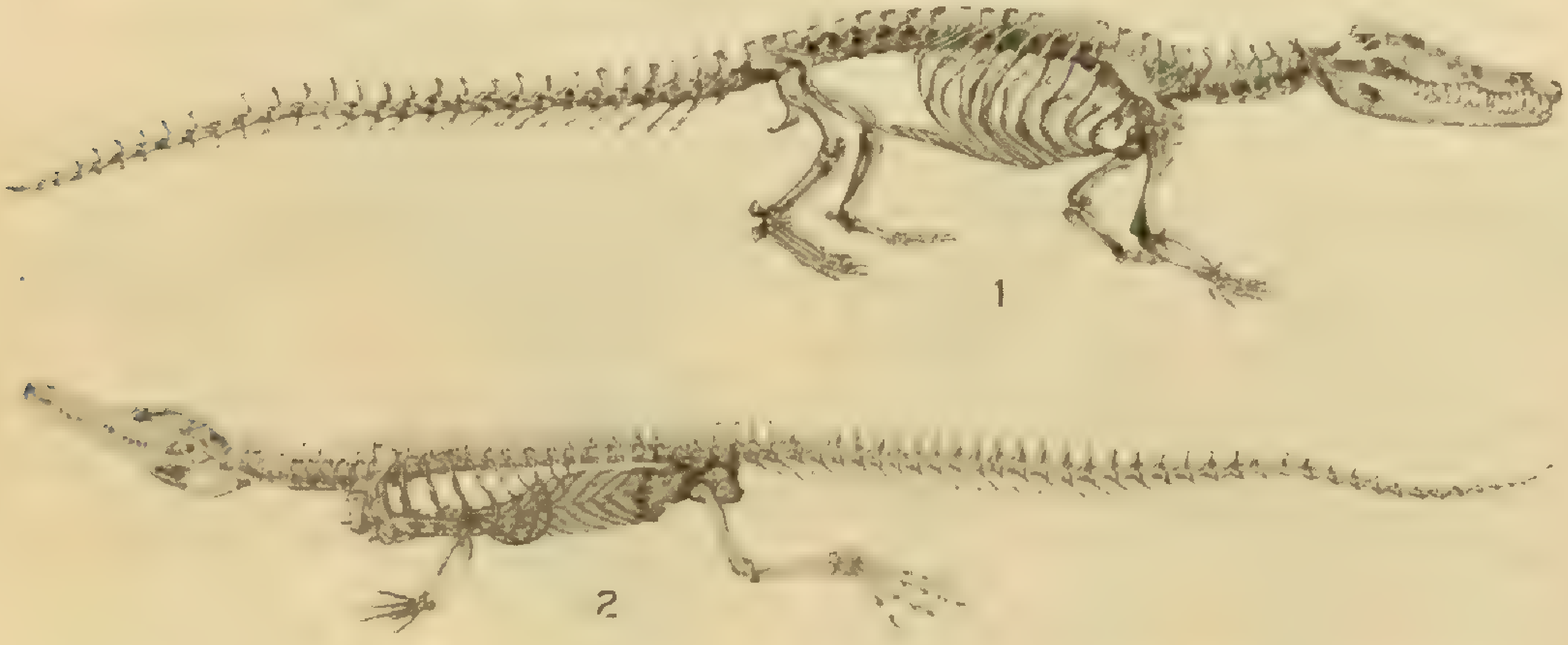


FIG. 13. 1, the skeleton of an alligator after Blainville; 2, skeleton of crocodile after Brühl, showing position of scapula.

---

[2] At this point the lecturer threw upon the screen a number of projections from X-ray photographs showing the limbs of the alligator in different attitudes. Only one of these is reproduced in the text.

alligator in the flesh, in which the parts surrounding the scapula have been dissected away, showing the scapula in the same position which is given by Blainville and Brühl. Any one who cares to verify the accuracy of my statements can easily do so. The scapula in the crocodile does not lie in the position which is given to the scapula by Mr. Tornier in his restoration and it certainly did not so lie in the *Diplodocus,* but the lateral processes of the anterior dorsal vertebræ as well as the upper external faces of the anterior ribs united to form a surface to which the scapula manifestly conformed itself when in position. Any one who carefully studies the vertebræ and the proximal ends of the anterior ribs will see that there is here provided by nature a plane adapted to the inner surface of the scapula.

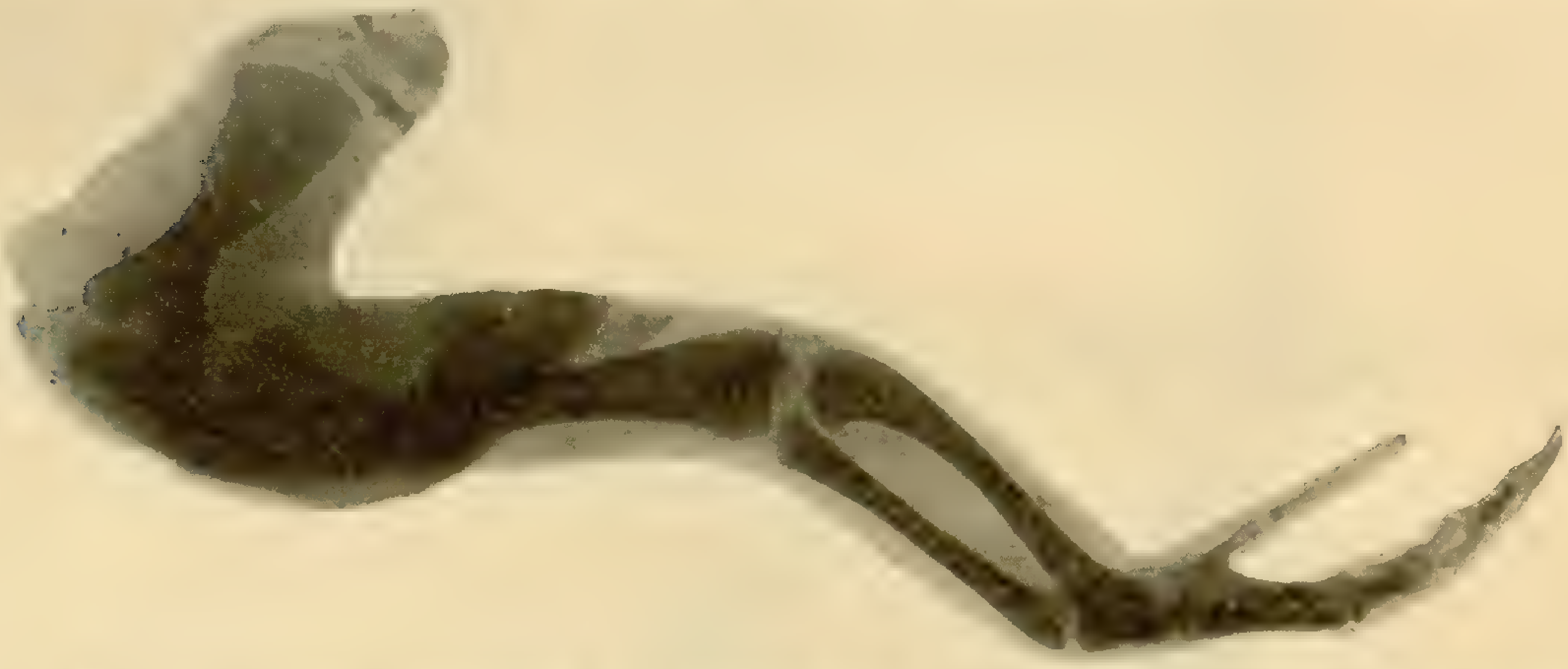


FIG. 14. X-ray photograph of scapula and humerous of alligator in position with foot thrown backward as far as possible. (Photographed by Dr. Geo. C. Johnston, Pittsburgh, Pa.) The scapula is not vertical.

For the sake of experiment I have placed the scapula in the position demanded for it by Mr. Tornier, and have swung the fore limbs into place as he demands that they shall be put (Fig. 15). The result is in every way amusing. It leads in the first place to the entire disarticulation of the humerus from the radius and ulna. But as a secondary consequence it leads to a rather remarkable result, which the Berlin critic did not think of. In the position which Professor Tornier demands for the elements of the fore limb, the foot must fall into a position with the toes turned inwardly, while put into the position which he demands for the hind limbs the toes of the latter necessarily point outwardly. The accompanying diagram (Fig. 16) shows you the position which the hind feet and the fore feet assume when placed as Professor Tornier demands they shall be placed. Now, attributing to the humerus backward and forward motion in a horizontal plane, you will see, as the dotted lines in the diagram show, the result which is reached when the humerus is thrown into a line parallel with the line given to the femur. The toes of the manus point inward and backward. The animal was "pigeon-toed" in front, while its hind feet were planted like those of a grenadier. The animal moved forward with the hind-feet, moved backward with its fore feet. If Tornier is right it must necessarily have been somewhat "balled up."

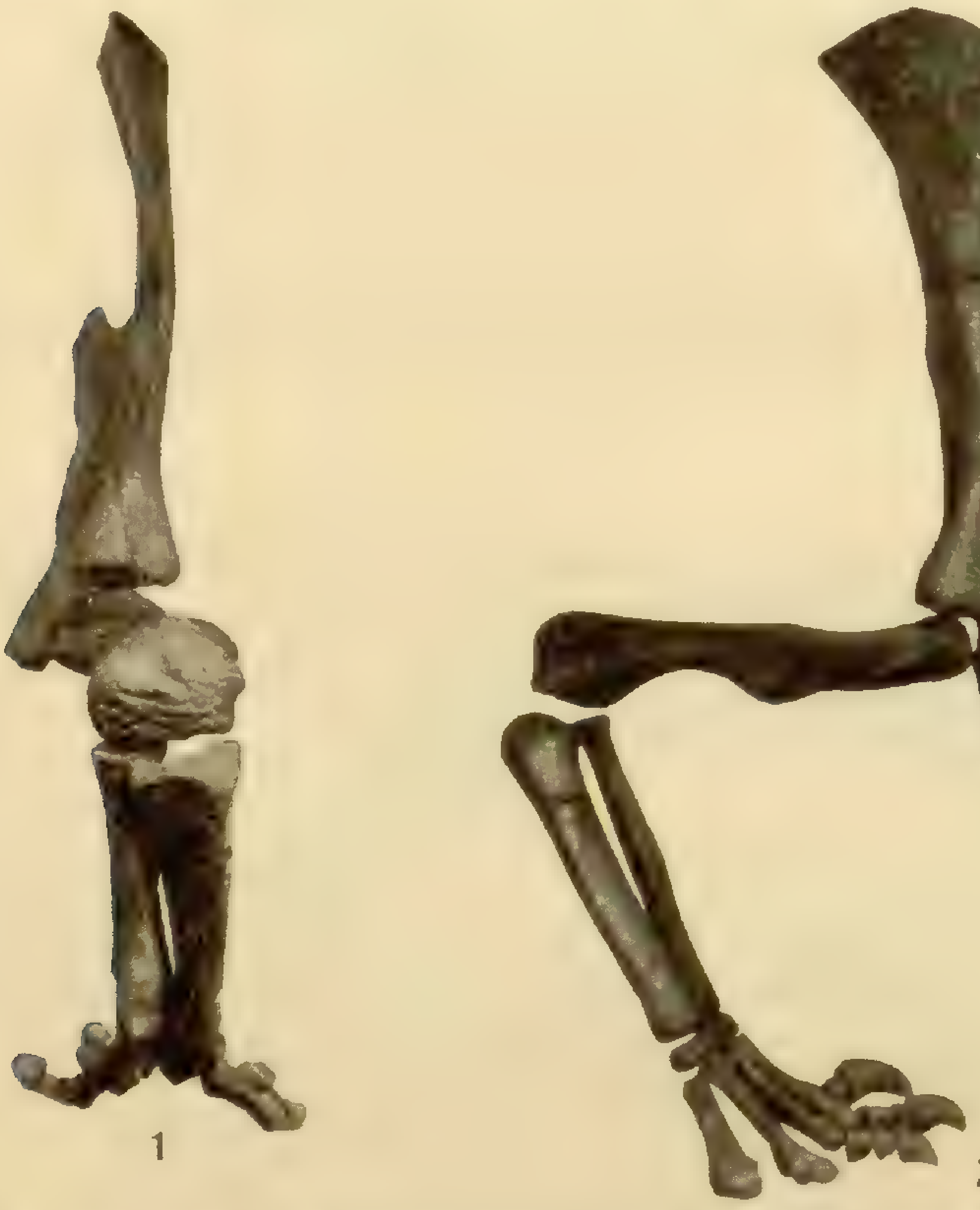


FIG. 15. 1, rear view of scapula and fore limb of *Diplodocus* mounted according to the Tornierian prescription; 2, side view of ditto.

The Berlin critic denies the possibility of a backward and forward movement of the humerus in the scapula in a vertical plane. As an actual fact, in the judgment of competent American investigators, the articulating surface of the humerus did thus move in the scapula, and the great projection on the outer side of the proximal end of the humerus, showing every evidence of having been provided with enormous muscular attachments, gave the animal the power to move the limb in the direction indicated, this projection being strictly analogous in function to the great trochanter of the humerus as it exists in the mammalia to-day. The statement that the downward projecting angle of the coracoid at its union with the scapula to form an acetabulum for the humerus precluded backward and forward motion in a perpendicular plane, as Tornier avers, is not borne out by an examination of the skeleton *in situ.* The humerus was capable of thus moving through a very long arc.

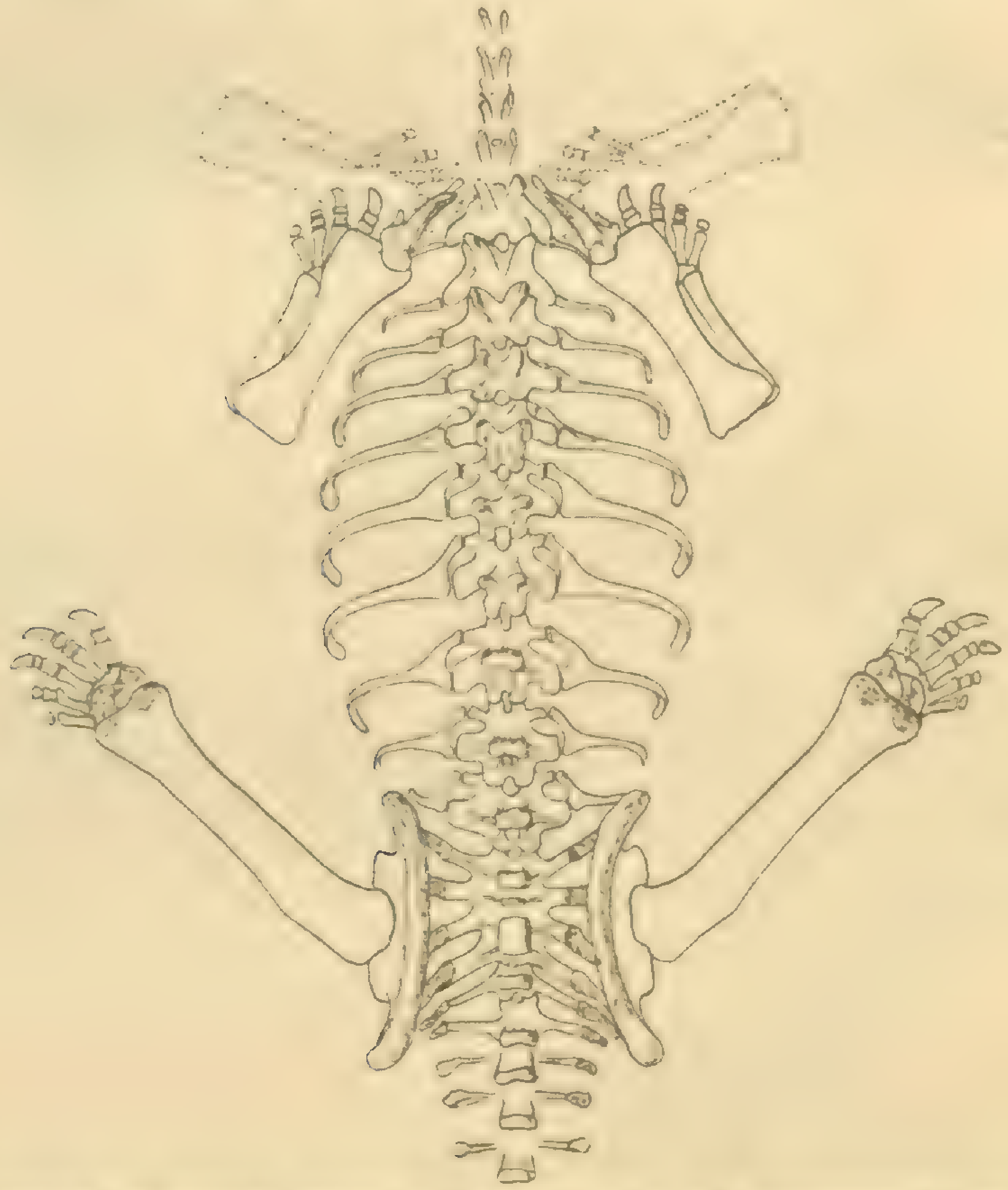


FIG. 16. Diagram showing position of the foot of *Diplodocus* when mounted and moved according to the Tornierian prescription.

Professor Tornier utterly ignores in his discussion a very important point, and that is, the structure of the ribs of the *Diplodocus* as compared with the structure of these parts in the recent reptilia. I throw upon the screen for purposes of easy comparison views of the ribs as they are arranged in recent crawling reptiles and of the ribs as they exist in the sauropoda, and more particularly in *Diplodocus* (Fig. 17). A glance at this diagram must be sufficient to show you the enormous differences which exist, and to reveal to one who has the least mechanical aptitude that the body, or "barrel," of the *Diplodocus* was constructed upon an ornithic rather than upon a lacertilian model. The articulation of the ribs does not lend itself to the idea that the animal progressed upon its belly.

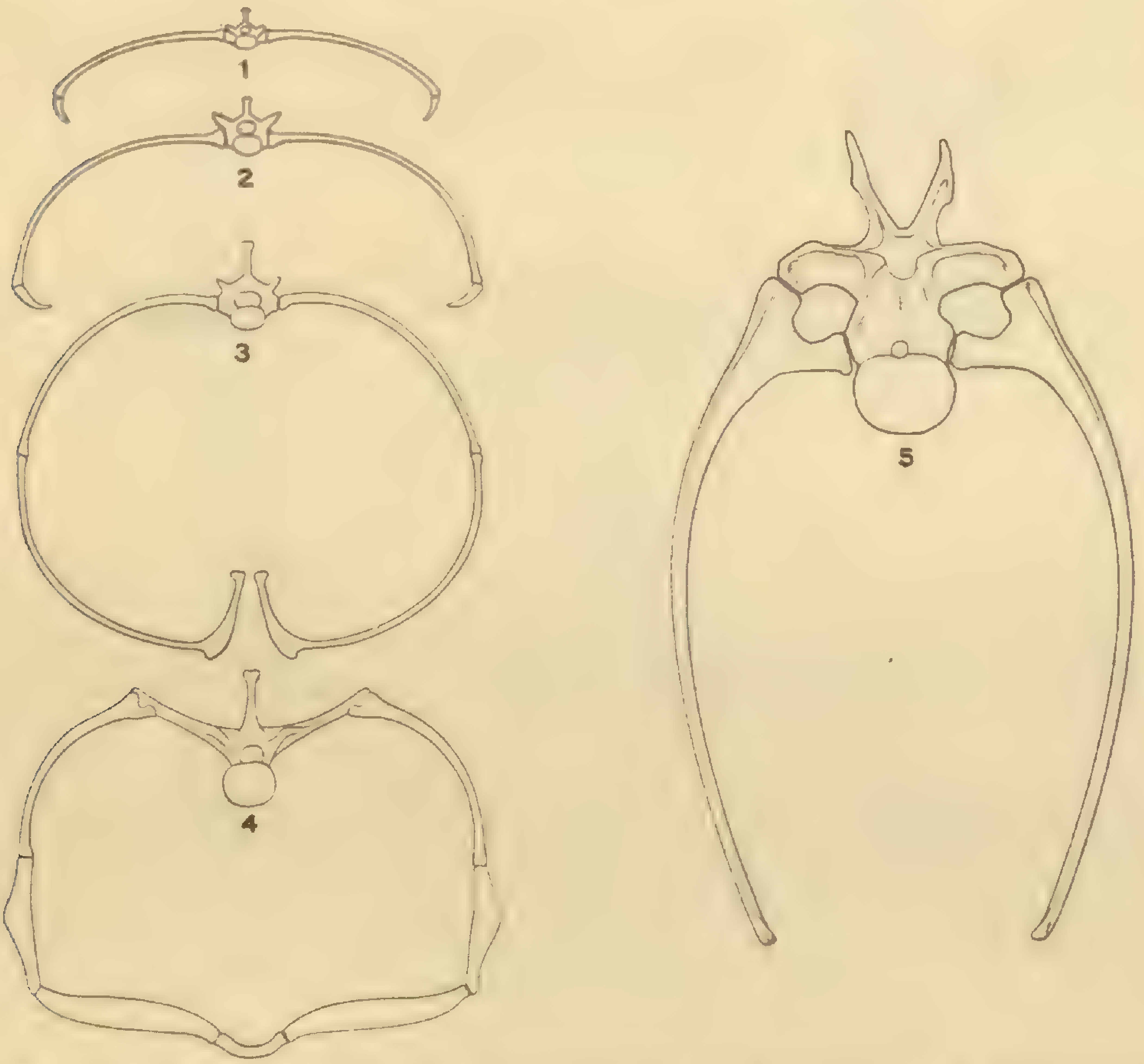


FIG. 17. Seventh dorsal rib articulated in 1, *Uromastrix;* 2, *Varanus;* 3, *Iguana;* 4, *Crocodilus;* 5, *Diplodocus.*

Professor Tornier says that the long tail of the sauropod dinosaurs was intended to be carried at full length upon the ground, to stiffen and guide the movement of the anterior portion of the body. He speaks of it as intended for anchoring the body, describing it as "ein

Verankerungsmittel." No doubt it did to a certain extent so function, but to regard it as having been an instrument for promoting, as Sternfeld indicates, a wriggling motion—"schlängelnde Bewegung"—is to attribute to the organ properties which it hardly possessed. The tail, while capable, no doubt, when the animal assumed a crouching position, of functioning as Tornier demands that it shall, must nevertheless have been to a very large degree used also as a support upon which the animal could when necessary prop itself, as upon one of the legs of a tripod, as undoubtedly was the case with the carnivorous dinosaurs, to which the sauropoda are not so very distantly related.

The theory, which has been proposed by Dr. Hay, that it was impossible for these huge sauropods to rear upward, seems to me to be one that any one who has carefully studied the movements of animals, and especially of reptiles (turtles excepted), must repudiate. We know that certain of the smaller lacertilia to-day, when in rapid motion, assume a bipedal pose. Professor Osborn in one of his papers has given us a reproduction of the figure of *Chlamydosaurus* in a running attitude, taken from an instantaneous photograph by Saville-Kent (Fig. 18).

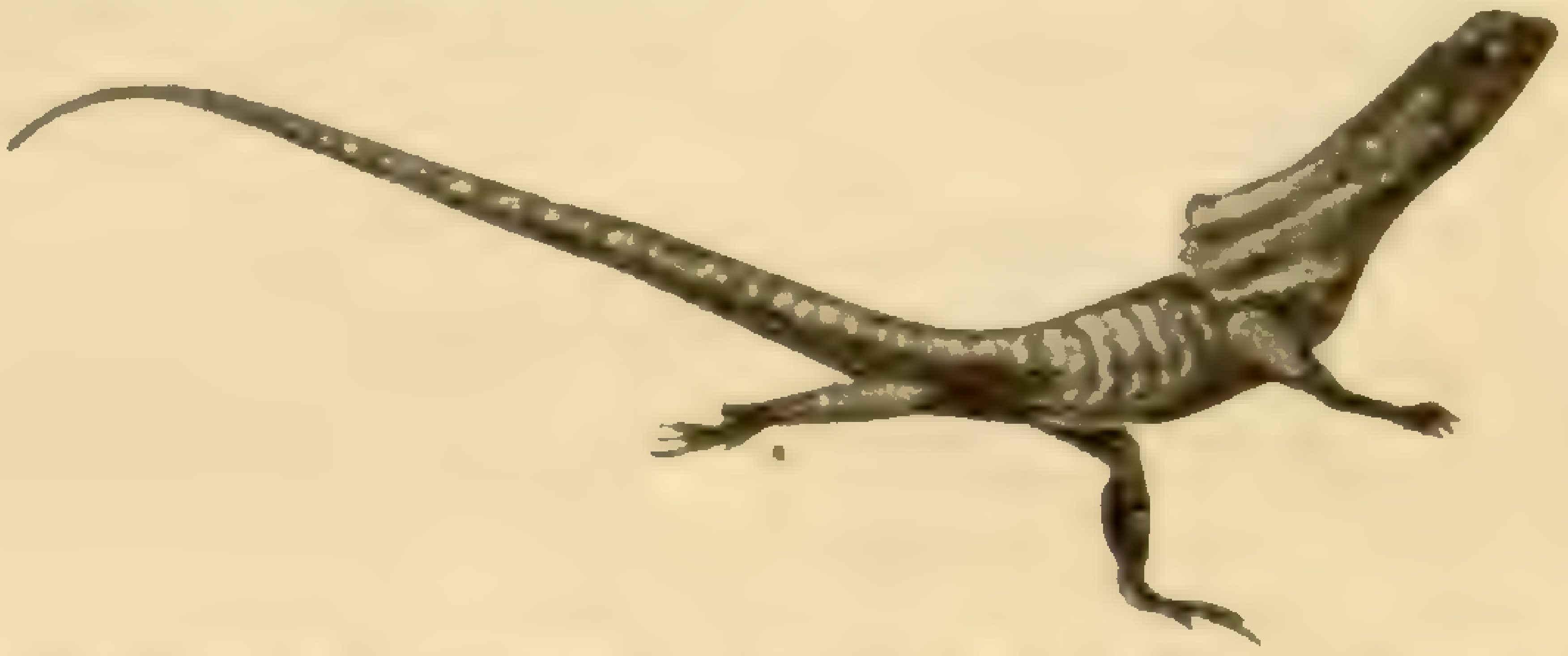


FIG. 18. *Chlamydosaurus* running. After Saville-Kent. Copied from Osborn.

Even more striking than the posture shown in this picture is the position constantly assumed by a well-known lizard of our southwestern and western country, *Crotaphytus collaris* Say. I regret that although I have had a number of these animals in captivity at our museum I never took the pains to have photographic snap-shots made of them when rapidly running across the floor. They assume when so doing a position in which the body is far more perpendicular than is the case in the picture before you, and they carry the tail even higher. Ordinarily these lacertilians crawl, trailing the tail behind them, but when alarmed they rise upon their hind feet and throw the tail upward, moving along with great speed. I do not advocate such a position for the tail of *Diplodocus*, but, simply because it is long, to declare therefore that it must have necessarily trailed with its whole length upon the ground, does not appear to me to be reasonable. Animals with tails relatively quite as long, and even longer, are known to-day to hold them elevated, and there was proportionately as much muscular power, as shown by the muscular attachments, in the tail of *Diplodocus*, as there is in the tail of a *Crotaphytus* or a *Chlamydosaurus*. To declare as Mr. Hay does, that these animals must have moved as crocodiles and could not by any possibility have raised themselves from the ground, does not appear to me to be logical. In fact, those of us who have hunted alligators know that in life even alligators raise themselves high upon their legs when running, and get away like a dog at a sort of a trot.

Tornier indulges in a lengthy criticism of the pose given to the feet in recent reproductions of the *Diplodocus* and demands that they shall be placed in a plantigrade position. He thus takes issue with Mr. Hatcher and with others who have carefully examined the subject. Professor Abel, of Vienna, in criticizing Dr. Hay's article, has very aptly pointed out that the manner in which the metacarpals articulate in the pes and manus indicates a more or less digitigrade position. Those of us who are familiar with the feet of the sauropod dinosaurs know very well that in their structure, as indicated by the facets of both the proximal and distal end, there is strong evidence that they were not plantigrade in the sense in which the feet of existing reptiles are plantigrade. I throw upon the screen a diagram showing the proximal ends of the metacarpal and metarsal elements (Fig. 19). They arrange themselves in a semicircle both in the hind foot and fore foot. This is less marked in the hind foot than in the fore foot. Such an arrangement of the metacarpals and metatarsals is significant, as has been pointed out by Hatcher and Osborn and is clearly shown by Abel. Sternfeld brushes Abel's criticism to one side, stating that it can be easily got rid of because the same arrangement exists in the feet of animals which are plantigrade. I would recommend Dr. Richard Sternfeld to more carefully study the anatomy of plantigrades. The structure of the feet of the sauropod dinosaurs differs immensely from that of the feet of all recent plantigrades and all the recent reptilia. We have evidence of a rather conclusive character as to the fact that the sauropod dinosaurs were decidedly digitigrade in the one existing specimen of a sauropod footprint, which is happily preserved, a figure of which I throw upon the screen (Fig. 20). You will see as you examine it that the animal must have been provided, as Professor Hatcher long ago pointed out, with a very large foot-pad, and that its track is not at all like the track of any of the recent lacertilia. The evidence of this footprint is impressive and ought to go a long way toward confirming the view, which I believe is the only view which we can maintain, that these animals were more or less digitigrade in the pose of their feet.

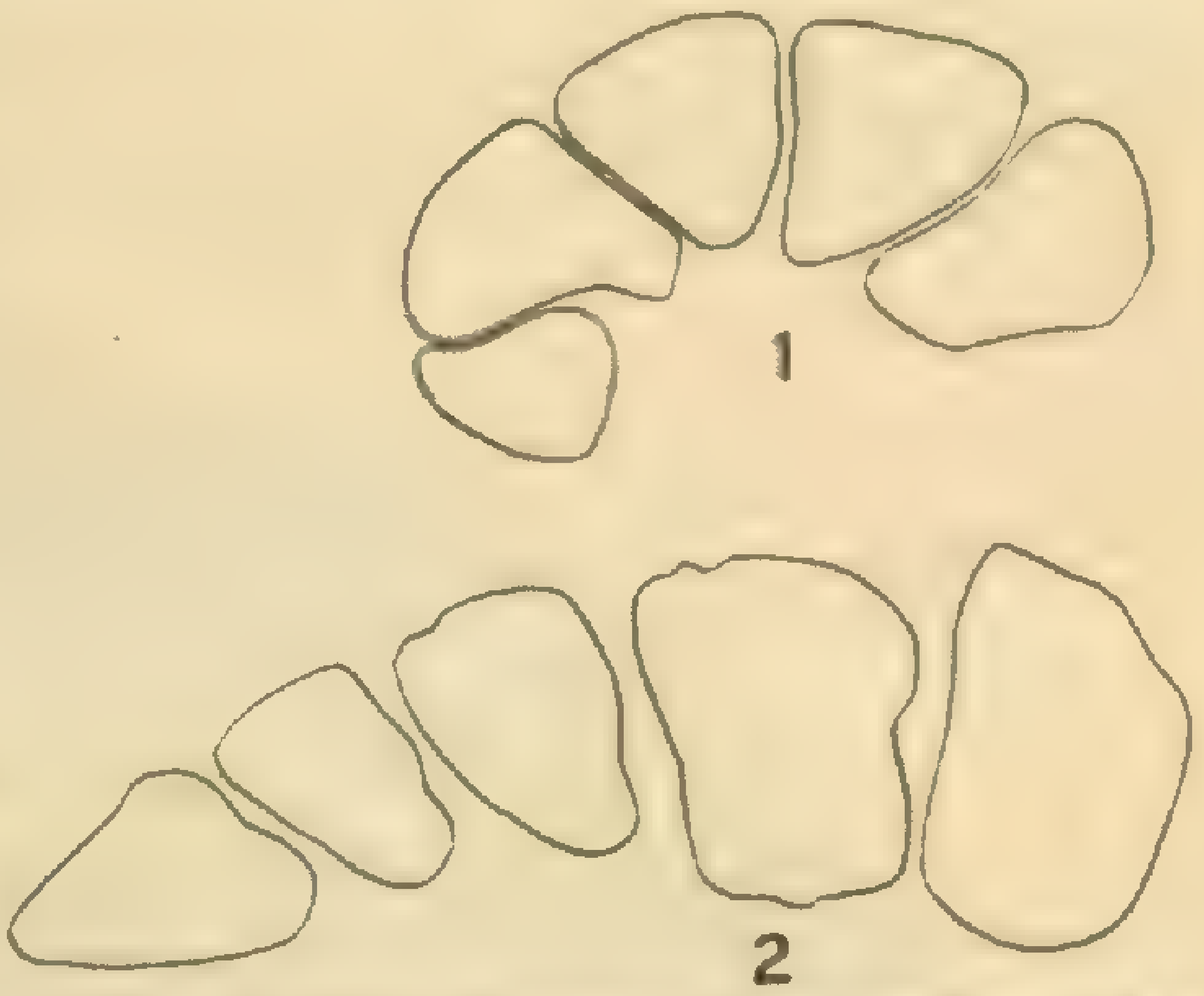


FIG. 19. Diagram showing arrangement at proximal end. 1, of metacarpals; 2, of metatarsals of *Diplodocus*.

The form of the limbs, long, straight and pillar-like, in this respect differing vastly from the limbs of the creeping lacertilia and crocodilia, suggests that they were intended to support a weight thrown upon them from above. The femur of the crocodile, as you know, is bent, and the femora of many of the recent lacertilians likewise show a distinct curvature of the axis. The same thing is true of the fore limbs, notably in *Varanus*.

The axis of the proximal end of the humerus in *Varanus* lies in a plane differing as much as forty-five degrees from the plane of the axis at the distal end. This is not true in the case of the sauropod dinosaurs. The limbs were intended to bear a burden placed mainly above, and their structure seems to plainly indicate this. It is in short impossible to articulate the limbs in such a position as to impart to the animal a crawling attitude. We have experimented a score of times and have tried different poses, only to come back again to the position which we have given to the reproduction of *Diplodocus* and which is the position that has generally been accepted by osteologists as the correct position for such animals when standing or moving forward. Our reproductions may be, as they have been contemptuously styled by Hay, "light-legged and straight-legged," but no one who has had the matter practically in hand has yet been able to suggest any way of escaping the conclusion that these creatures were at all events more or less "straight-

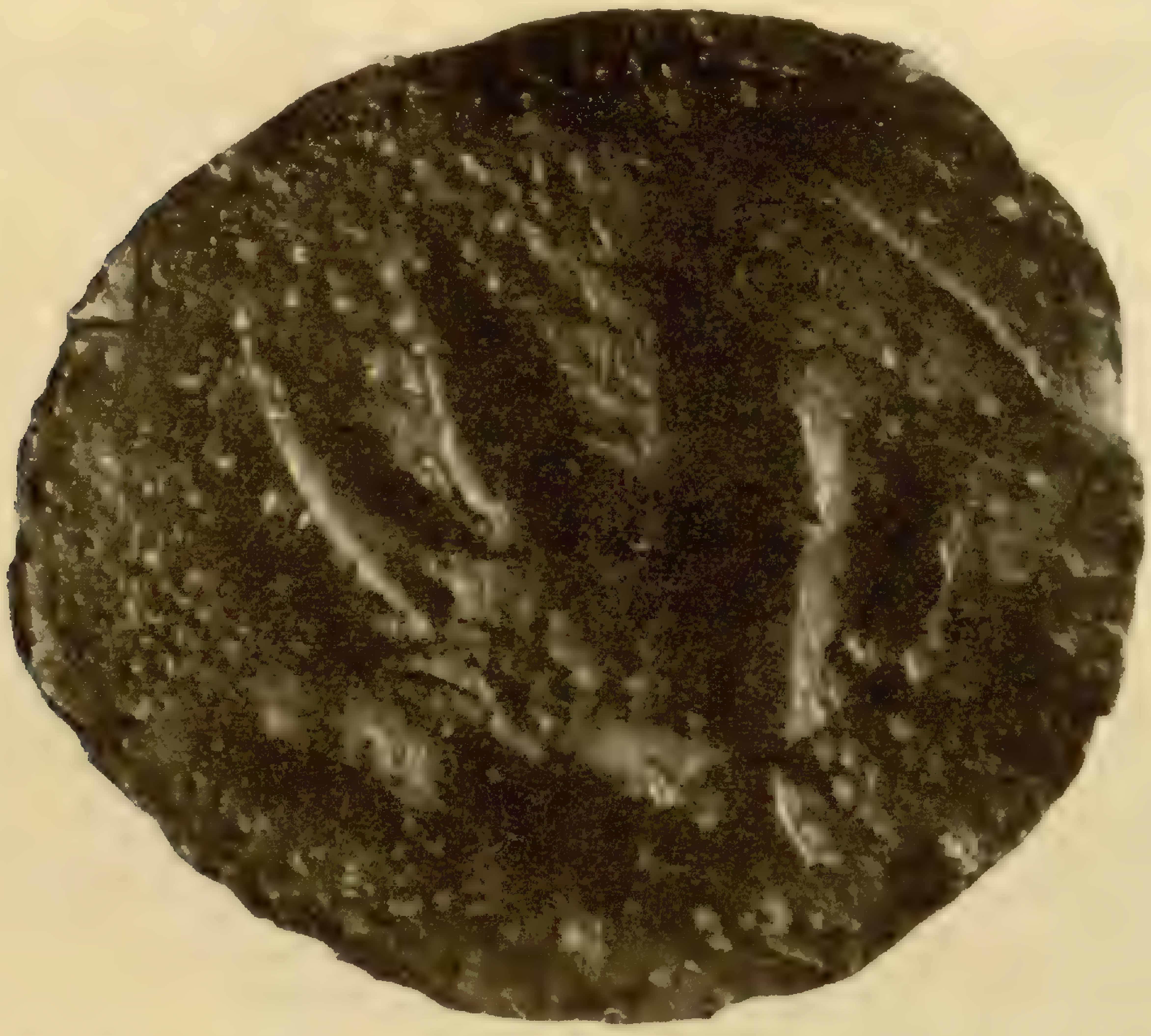


Fig. 20. Footprint of sauropod dinosaur. Specimen in the Carnegie Museum.

legged.'' For their ''light-legged'' qualities nature is solely responsible, though I fail, standing before these huge bones, to see why anybody should so describe them. Students of the lacertilia and of the testudinata may sneer, but it is beyond possibility to adopt the suggestions which they from time to time make, that those of us who are engaged in studing the dinosaurs shall squeeze these creatures into the forms with which they are familiar. The critics possibly do not realize that weeks and months and years of study have been spent by those who have been charged with the task of assembling these remains, and that the prescriptions, which they now furnish, have been already tried without their suggestion, and have for good reasons been found wanting. It is easy for a knight of the quill, who has never practically attended to the matter, to find fault. The latest attack upon those who have been making a special study of the sauropod dinosaurs has only served in the mind of the speaker to prove the correctness of the careful work which has been done in the past by students on both sides of the Atlantic. Evolution has had something to do since the sauropod dinosaurs walked the earth, and to say simply because the lacertilia of the present day creep and crawl that in Mesozoic times there were no reptiles which walked, is to go further than the facts seem to warrant. The pinnipedia and the cetacea live in the waters: it does not necessarily follow that their ancestors were aquatic in their habits and that their limbs were like those which they possess. Because snakes are to-day without feet or with only vestigial feet, it does not follow that the ancestral forms in remote antiquity moved as they move. Because a *Varanus* crawls to-day it does not necessarily follow that a sauropod dinosaur crawled. There is every evidence that they did not crawl, but that the restorations of Marsh, Osborn, and others are substantially correct in many important particulars. It is ''a far cry'' from the crocodilia, which, by the by, existed contemporaneously with the sauropoda, and the genera *Brontosaurus, Morosaurus,* and *Diplodocus.*

The Tornierian hypothesis may be dismissed, I think, as not within the range of the possible. It has, as one of my learned paleontological friends in Europe jocosely remarked to me, "only this feature to recommend it, that it accounts for the speedy disappearance of the sauropoda, because if true, their lives must have been spent in indescribable agony, every joint being dislocated."

Both Dr. Hay and Professor Tornier indulge in speculation as to the food of *Diplodocus.* Tornier emphatically repudiates the idea that the animal was herbivorous and suggests that it was piscivorous. Sternfeld pictures it as squatting on the banks of streams and feeding on snails, bivalves, and amphibians. Hay approves of the suggestion of the present speaker, that *Diplodocus* may have fed upon algæ. In this field we are all more or less left to our imaginations, and one man's guess is as good as another's. In view of the fact that cycads were numerous at the time when the *Diplodocus* and its allies lived and died, it may not be improper to renew the suggestion that possibly these plants furnished the food of the sauropod dinosaurs. However the terminal buds would have been poor fodder, being woolly and harsh, and the leaves are as stiff as wires and could not have been masticated by such teeth as the *Diplodocus* possessed. On the other hand the interior of the stems of the cycads, "sago-palms," is in all recent species a veritable mine of nutritious food, and was presumably the same in the ancestral forms. While the comparatively feeble dentition of the Sauropoda would not have been of much use in getting at these supplies of starchy food, the heavy claw-like armature of the feet was quite equal to the task of ripping open the thin outer bark of the stems, and this accomplished, a single cycad stem of some of the larger species would have furnished a good meal of soft food capable of satisfying the hunger even of a *Diplodocus.* This suggestion has been freely discussed by the speaker with Dr. N. L. Britton of the

New York Botanical Garden, and seems plausible. It is thrown out as a hint worthy of consideration. If the terminal end of a cycad could have been torn away this also would have given access to the mass of food in the stem. The feeble dentition hardly seems equal to the task of tearing away this upper growth, but if it was, we then might have a reason for the great elongation of the neck.

Before I conclude these remarks I desire to say that I am not without hope that recent discoveries made by the Carnegie Institute will tend to throw a flood of light on the whole subject. We have found what paleontologists have been searching for for forty or fifty years, three skeletons of sauropod dinosaurs lying articulated where they died. They are imbedded in hard sandstone, the work of removing which from the bones must involve a vast expenditure of time and effort; but in one case at least we know already that the vertebral column lies in position, articulated from end to end. Apparently hardly any disturbance has occurred and the bones even to the minutest tuberosities and rugosities are as perfect as when the animal died. The sternal ribs are present. When we succeed in carefully working out these huge skeletons from the surrounding matrix we shall probably be able to clear up some of the disputed points in the osteology of the sauropod dinosaurs.

ANATOMICAL CHARACTERS IN THE EVOLUTION OF PINUS[1]

IRVING W. BAILEY

HARVARD UNIVERSITY

Pinus is the oldest genus of the conifers and the most important and interesting, whether considered from the botanical, economic or aboricultural standpoint. Occurring as it does in many species throughout the whole northern hemisphere, from it are derived many of the most valuable timbers and extractable products of commerce. In accordance with the general impression, that flourishing genera are modern, since they show an obvious adaptation to existing conditions of environment, it has been assumed that *Pinus* is of comparatively recent origin and marks the last word as it were in coniferous development. Recent investigations however of the occurrence of *Pinus* in the American Cretaceous, show that in the lower levels of that epoch, species of pines were apparently much more numerous than they are at the present time. It is accordingly apparent that so ancient a genus as *Pinus* and one so richly endowed with an abundant modern progeny supplies a particularly favorable subject for evolutionary investigation.

It has been the practice in the past to arrange plants systematically on the basis of external characters alone, chiefly on the superficial features of their floral organs and leaves. In the case of so ancient a genus as that under consideration, this procedure has peculiar difficulties connected with it, since in the tremendous period of time during which it has been in existence, its external characters have undergone many puzzling changes. The internal structure of the genus however has shown less range of variability and greater constancy in definite lines. On account of the long geological range of *Pinus,* anatomical characters, notoriously more constant than any others found in the higher plants, have had time to become considerably diversified. As a result of the action of this principle, it is much more easy to differentiate two such *species* as *Pinus strobus* Linn. and *P. palustris* Mill. from one another anatomically than distinct Cupressineous *genera* such as *Chamæcyparis* and *Thuya.* This arises from the fact that the Cupressineæ, to which the two last-named genera belong, are of very recent origin compared with many of the species of *Pinus.*

---

[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 22.

Before attacking the anatomical differences which mark the main lines of evolution in pines, it will be well to consider the artificiality of the groups into which they may be divided by the use of solely superficial characters. Such characters are the number of leaves in the fascicle, the deciduous or nondeciduous nature of the leaf-sheath, the texture of the cone-scale and the relative size of the seeds. Quinate leaf fascicles formed, for example, a very satisfactory basis for the classification of pines before those of the southern United States and Mexico became known to science. In Europe, Asia and northern North America, the possession of quinate leaf fascicles is a constant character of soft pines of the *Strobus* and allied sections. In the southern region of North America, however, are found hard pines such as *P. Torreyana* Parry, *P. arizonica* Englm. and *P. Montezumæ* Lamb. with leaf fascicle containing five leaves. On the other hand, a *persistent* leaf sheath such as is a feature of the hard pines is absent in *P. chihuahuana, P. leiophylla* and *P. Lumholtzii,* quite typical pines of the group in other respects. Nor is the texture of the cone-scale or the position of the apophysis on the umbo, characters which are used to distinguish the larger groups of Pines, any less exempt from disconcerting exceptions. The American nut-pines, as well as those of

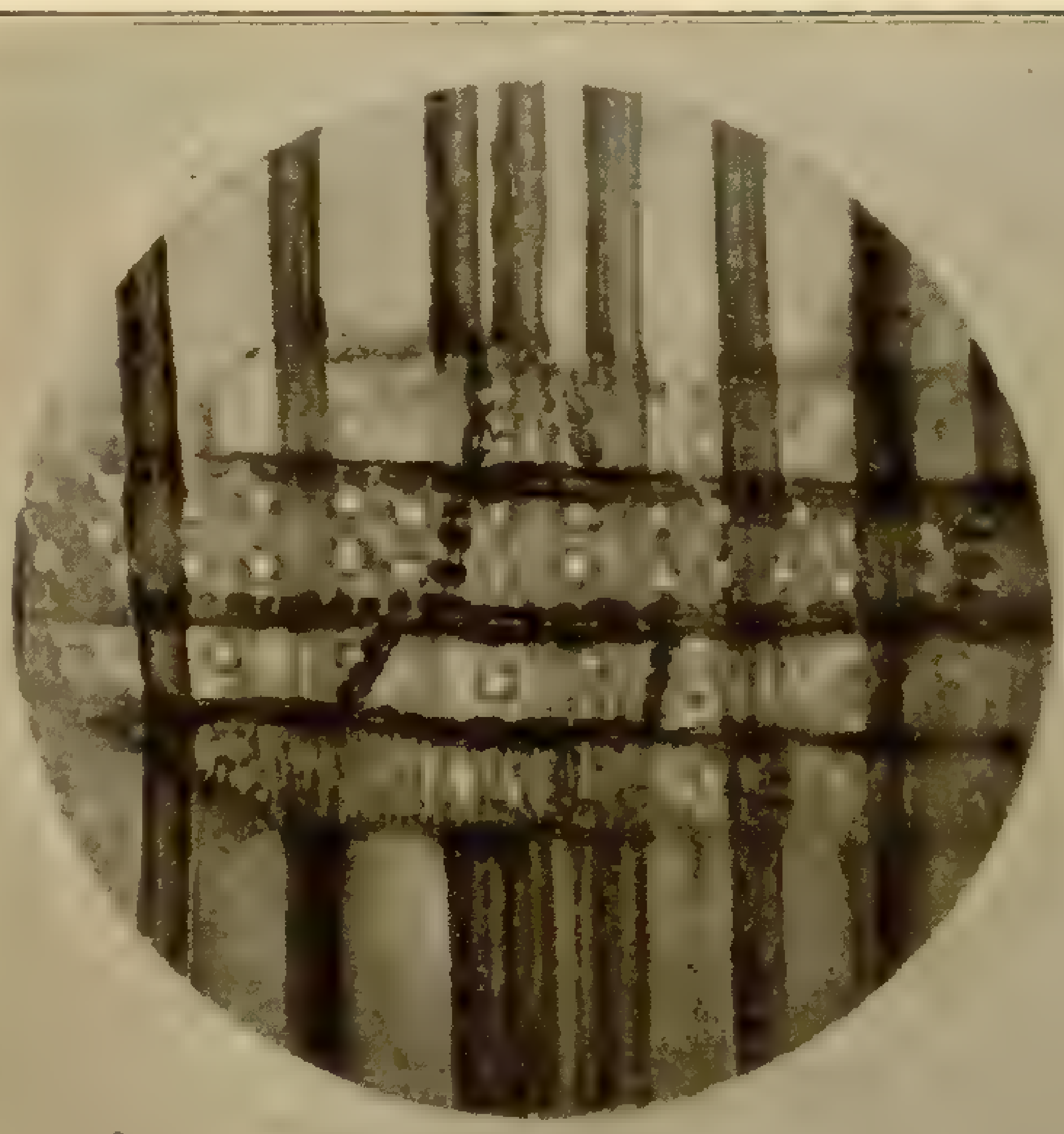
Asia, although belonging to the soft pine series have the thick cone-scales and median dorsal umbo of the hard pines. Nor is the nut-like character of the seed a constant character, for the nut-pine of Italy is a hard pine, while those of America and Asia are soft pines. If we seek for really dependable criteria for the classification of pines, we have to go below the surface. The single leaf-trace, for example, is absolutely constant throughout the soft-pine series as is equally the case with the double foliar bundle in the hard-pine series. Similarly, the soft pines are characterized by a single row of resin-canals in the first year's growth which is duplicated or further multiplied in the hard pines. Englemann has further indicated the value of the number and position of the resin canals in the leaf for diagnostic purposes. An extremely important anatomical character for the separation of the two great series of living pines is the nature of the tracheid-like cells on the margins of the wood-rays. The nature of the pitting in the tracheids of the wood and the central cells of the wood-rays likewise supply valuable criteria for the establishment of smaller subdivisions. It will be inferred from what has been said, that anatomical characteristics in the case of *Pinus* are very constant in broad lines and consequently are for the establishment of a natural classification, indicating the evolution of the genus, of the greatest value. External characters, on the other hand, are much subject to variability.

Two main series of pines, the hard pines and the soft pines, may be clearly recognized, in accordance with anatomical characters. For example, the groups of which *P. strobus* Linn. and *P. silvestris* Linn. are types, are quite distinct. The latter species is characterized with the remaining hard pines, without exception, by the double foliar fibrovascular bundle, two or more rows of resin canals in the first ring of woody growth and dentate or reticulate marginal tracheids of the wood-rays. The former species, together with the other soft pines, has throughout the single leaf bundle, the single row of resin canals in the first woody ring and smooth-walled marginal ray-tracheids.[1] These two great races of pines, which may be traced from the Cretaceous to the present, may be subdivided on the basis of other characters, internal and external. Within the subdivisions differences in floral and foliar characters are much less variable than in the main lines.

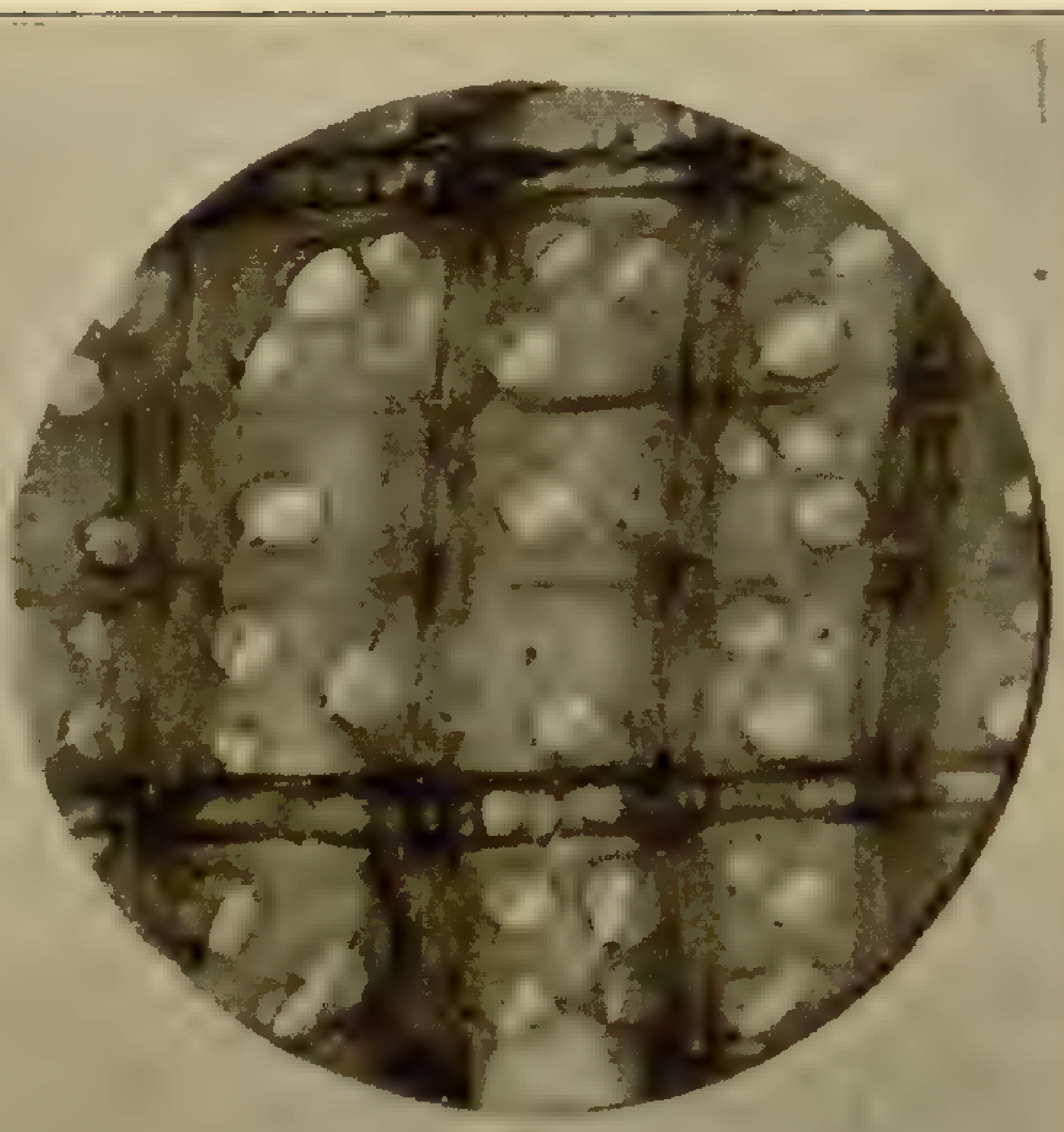
The nature of the parenchyma in the wood rays and the characters of the pits which connect them with the tracheids are features of considerable evolutionary and diagnostic importance in the various smaller subdivisions of the genus under consideration. For example, among the soft pines we find a group illustrated by the nut pines and foxtail pines of the United States, and by the nut pines of Asia (*P. Gerardiana* Wallich. and *P. Bungeana* Zucc.), which are characterized by the possession of thick-walled ray parenchyma, with very small lateral pits having distinctly circular borders (Fig. 1). These pits are usually four in each "cross field" (a cross field is the area of intersection of a ray cell and a tracheid) and quite distinctly separated from each other. The opening on the side of the tracheid is slit-like and often exceeds in length the diameter of the pit. The opening on the side of the ray cell is circular or lenticular and smaller or nearly equal in diameter to the border. In most of the nut pines and fox-tail pines these pits are rather uniform in size and in diameter, the same as the lateral pit in the marginal tracheids of the rays. In *P. Bungeana* of China the pits are of large size, with widely lenticular openings and more approximated than in the other nut pines. Small lateral pits such as those just described with distinct circular borders are characteristic of the ray cells of most of the conifers and are conveniently termed "piciform."

---

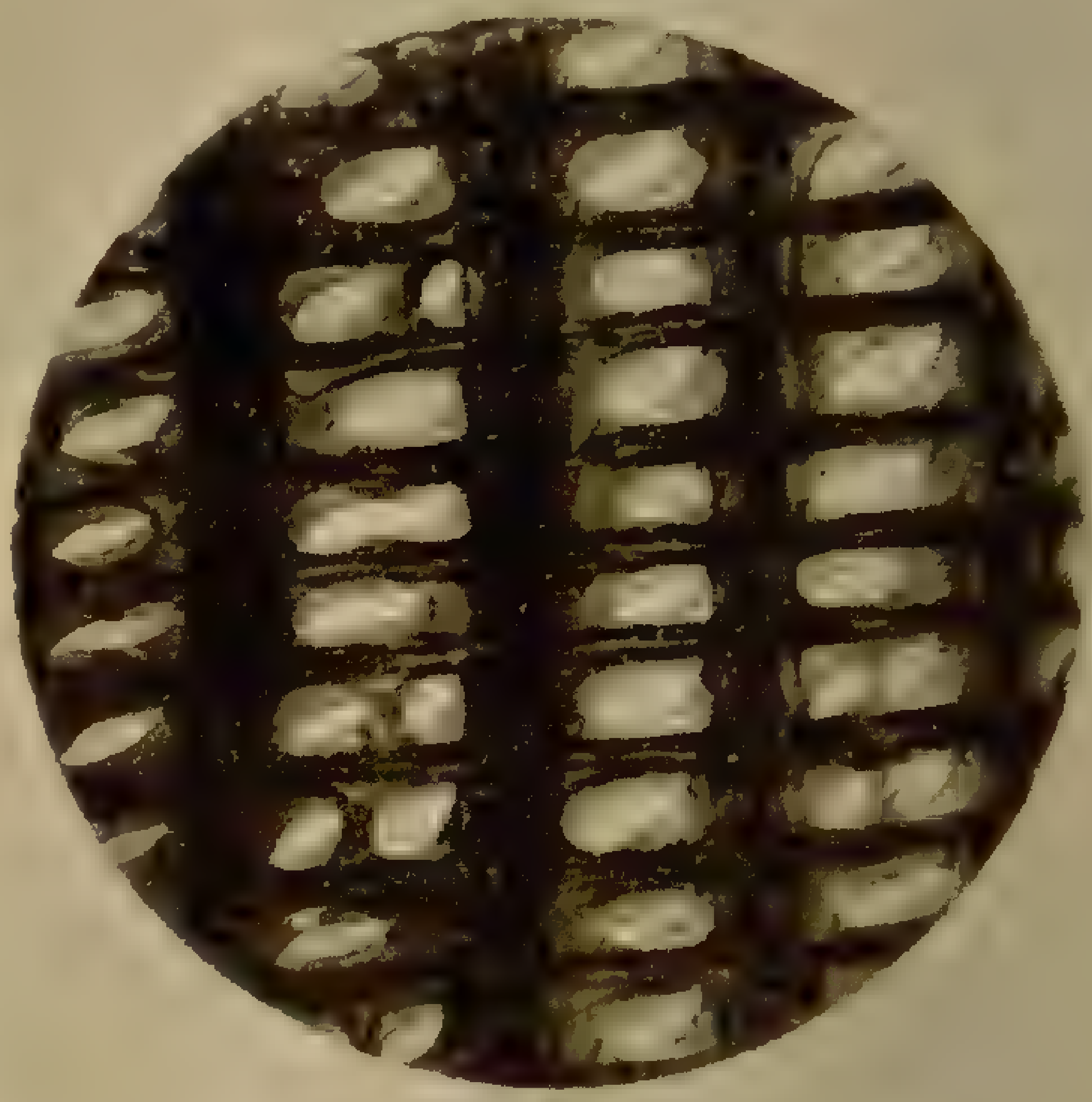
[1] Smooth-walled except for occasional spiral markings (see Fig. 1) which are quite distinct from the heavily sculptured reticulate and dentate marginal tracheids of the hard pines.



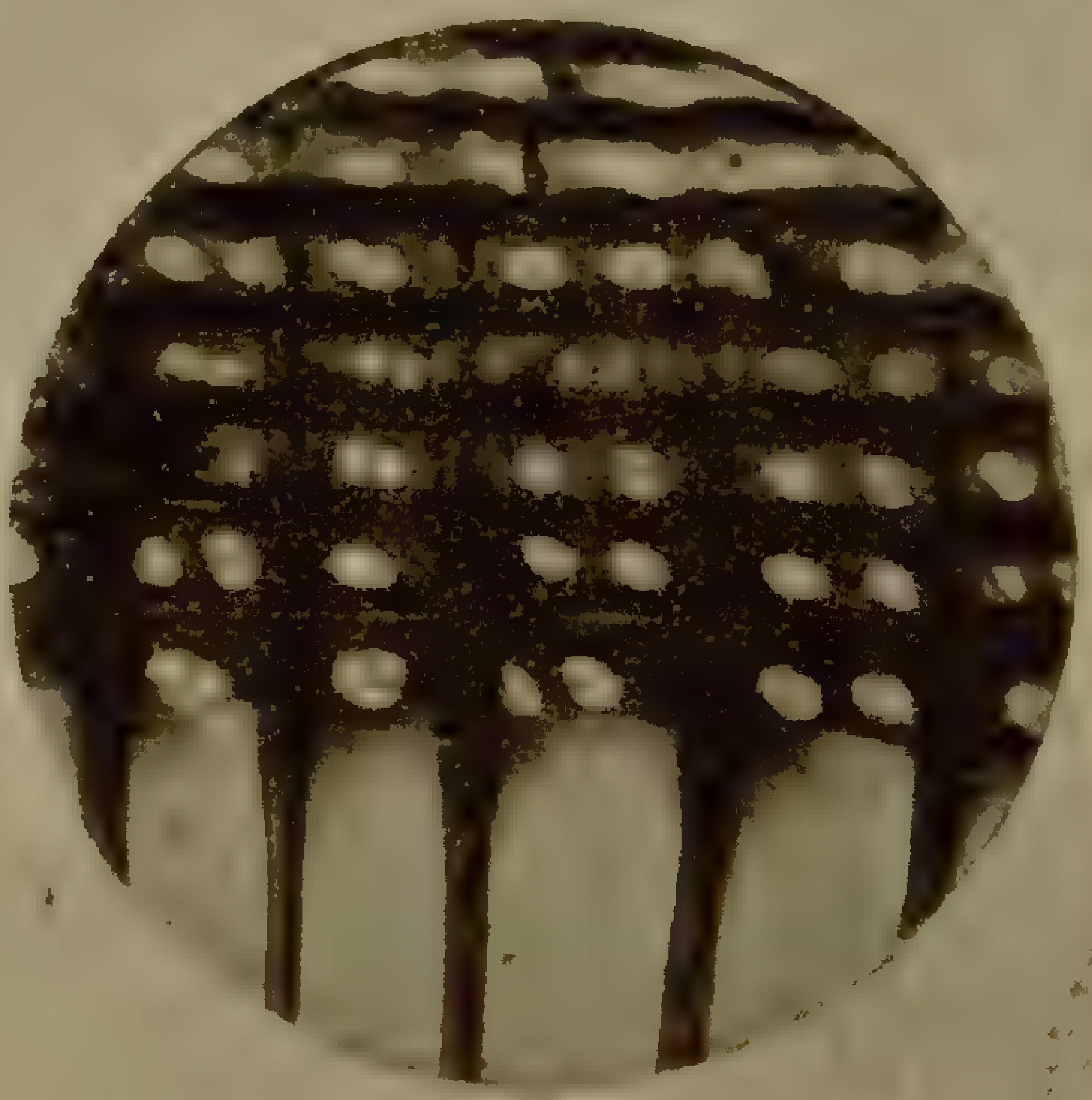
1



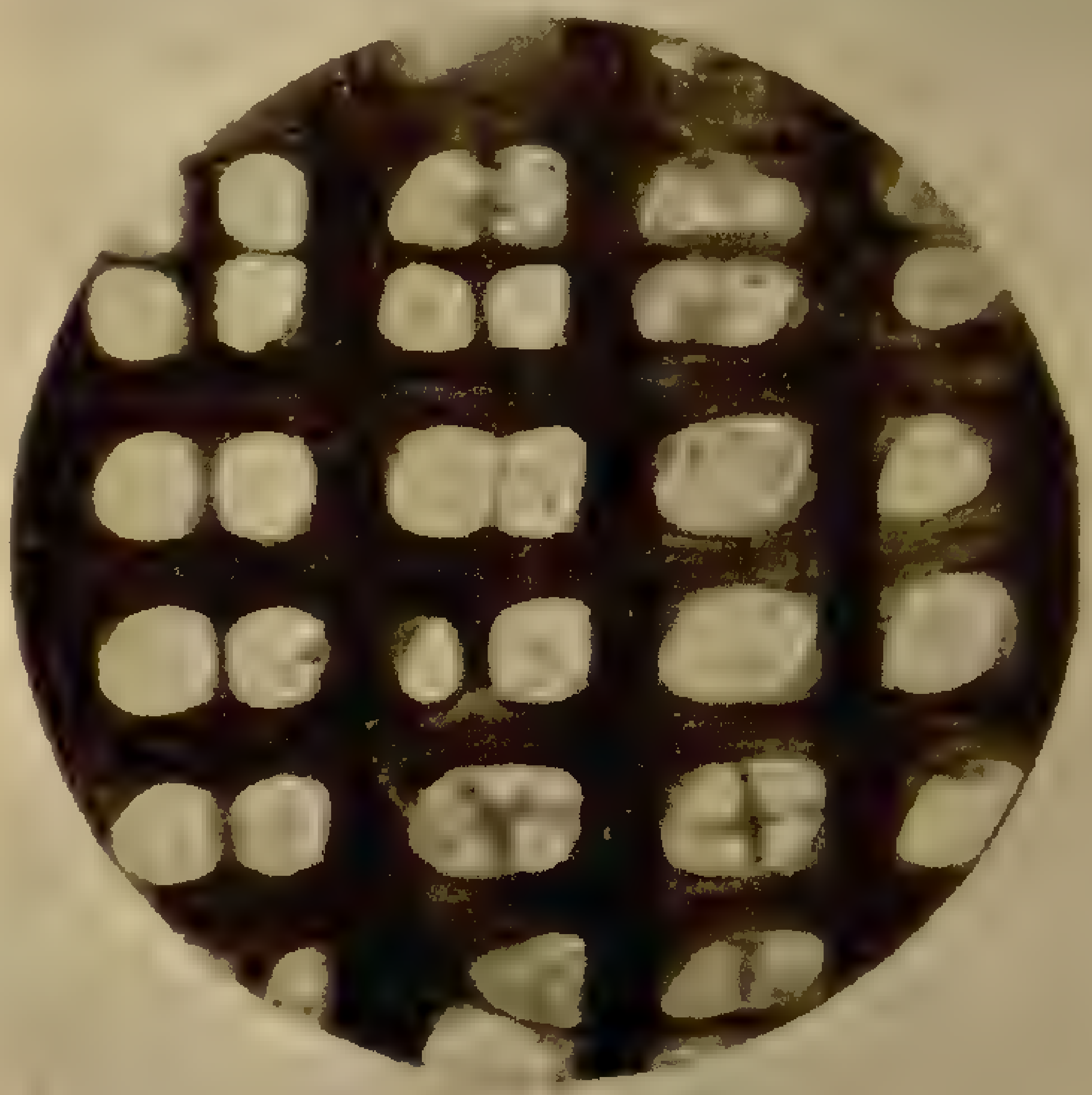
2



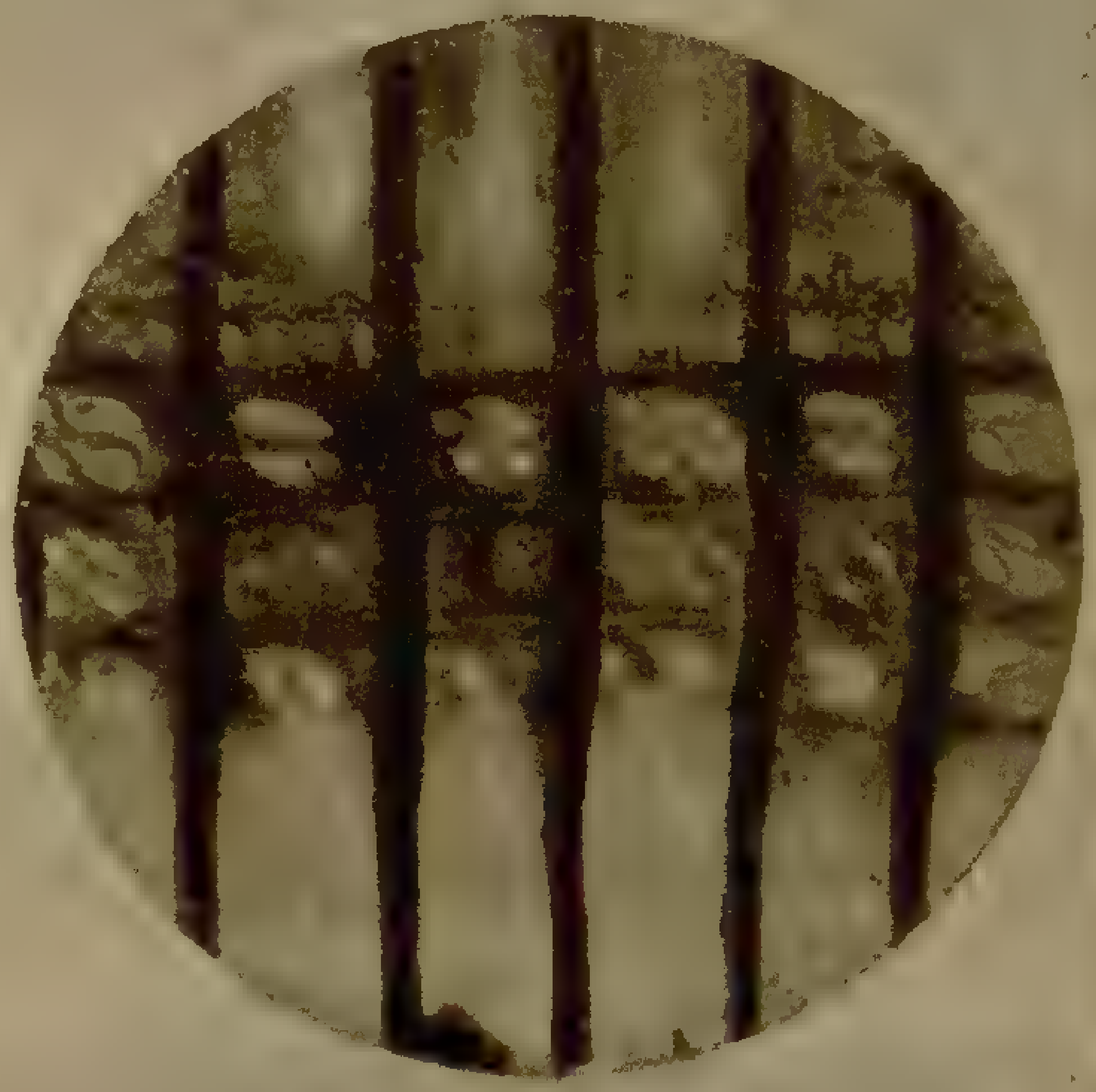
3



4



5



6

EXPLANATION OF PLATE

FIG. 1. Radial section of *Pinus Balfouriana*, showing the thick-walled character of the ray parenchyma, the characteristic piciform pitting of the nut pines, and a *ray tacheid with spiral markings* which are characteristic of this species. × 500.

FIG. 2. Radial section of the root of *Pinus tæda*, showing the variation in the size of the pits, the distinctly bordered outlines and the increase in width of the oriface with increase in size of the border. × 300.

FIG. 3. Radial section of *Pinus Ayacuite*, showing large pits with distinct circular borders and their fusion in places into large pits with oblong borders. × 300.

FIG. 4. Radial section of *Pinus Lambertiana*, showing the formation of one or two medium-sized pits by the fusion of 2–4 small pits. The fusion has progressed most rapidly on the tracheid side and the ghost-like remains of the parenchyma partitions may still be seen. × 200.

FIG. 5. Radial section of *Pinus flexilis* James, showing on the upper side the process by which four medium-sized pits, produced by fusion, are fusing in turn into one or two medium-sized pits. In the center two medium-sized pits are fusing into a single large pit, and at the bottom two pits, in which the tracheid wall has fallen away before the parenchyma wall, may be seen. The ghost-like remains of the divisions of four and five small pits are still visible. × 300.

FIG. 6. Radial section of *Pinus palustris*, showing piciform pits, the increase in size of these, and their fusion into irregularly shaped pits of many forms. × 500.

In the majority of the hard pines of the United States, we find ray pits somewhat similar to those of the nut pines. There are present one to eight small pits in each cross-field (Fig. 2). These pits, however, are very variable in size, number, form and structure. In some species, and in certain regions in almost all species, small piciform pits may be found (Fig. 6) occurring with these. In most species are pits with circular borders of larger size and wide slit-like or lenticular orifices (Figs. 2 and 6). In places these pits become approximated and the borders fuse to form a single irregular border surrounding an elongated irregular pit. In certain species such as *P. palustris* Mill., *P. Murrayana* A. Murray, *P. tæda* Linn., etc., numerous pits of large size may originate in this way. These are often crescentic, long oval, sausage-shaped or widely lenticular in form (Fig. 6). In hard pines we see two distinct lines of specialization in the formation of large pits, a tendency for the piciform pits to simply increase in size or a tendency for pits of large dimensions to be formed from the fusion of smaller ones. Hand in hand with the transition from small piciform to large pits there occurs a transition from thick to thin-walled ray parenchyma cells. Certain Pines (*e. g., P. Murrayana* A. Murray) show all gradations from thick-walled cells such as are characteristic of nut pines to very thin-walled cells, such as occur in the rays of *P. strobus* Linn. It is of interest to note that pit fusions take place equally in both thick- and thin-walled ray elements. Either the thick- or thin-walled type of cell may predominate in the ray of the various hard pines. In the seedling and the woody axis of the cone of such pines, we find the ancestral piciform type of pitting well represented, and in the cone-axis in particular the ray parenchyma is thick walled.

In both the hard and soft pines there is a group characterized by the possession of one or two very large pits in each cross-field (Figs. 3 and 5). In places, however, these may be represented by several small pits, and transitions may be found showing the development of these large pits from the smaller ones by fusion. In Fig. 5 is seen a condition characteristic of *P. strobus* Linn., *P. silvestris* Linn., *P. Laricio* Poiret., *P. Thunbergii* Parl., *P. Koraiensis* Sieb. et Zucc., *P. resinosa* Sol., *P. Cembra* Linn. and other pines with large lateral ray pits. In the upper part of Fig. 5 the stages in the development of two large pits from four small ones may be made out, while in the central region appears the origin of a single large pit from two smaller ones. In the lower part of the same figure may be seen instances of multiple fusion, such as are particularly characteristic of the soft pines, where the pit openings on the side of the tracheids often fuse before those on the side of the ray, so that the ghost-like relic of the separating ray wall may still be observed. In Fig. 4 is seen a condition, which may be considered to illustrate the formation of pits of medium size in Fig. 5. One or two rather small pits are being formed in most cases from the fusion of from two to four very small piciform pits. In Fig. 3 is seen a condition characteristic of certain soft pines (*P. Avacuite* Ehrenberg, *P. albicaulis* Englm., etc.) where the large-bordered pits have formed and are fusing in places to form elongated pits with oval outlines. The large pitted soft and hard pines show in the seedling a reversion to the ancestral condition of numerous small pits and in their cone-axes piciform ray pits are characteristically present. Such pines have ordinarily thin-walled rays cells, with the exception of such intermediate species as *P. Lambertiana* Doug. and *P. Ayacuite* Ehrenb.

With this review of the ray pitting in modern pines, it will be apparent that in the nut and fox-tail pines we have exclusively piciform pitting in the lateral walls of the ray. This condition is of interest because it perpetuates the type of pitting which has been invariably found in the rays of Cretaceous pines as well as in

Prepinus Jeffrey, which must be regarded as a very antique representative of the pine-like conifers. This is particularly significant on account of the other ancestral features presented by the nut pines. In both the hard and soft pines of the present epoch we find a gradual transition from the thick-walled rays cells with abundant piciform pitting of the ancestral type to thin-walled cells with few large compound pits. These large pits have been formed for the most part by the fusion of smaller pits, although in some instances they appear to have been derived by the simple enlargement of the piciform type of pit. It is of interest to note that the succiniferous pines, which gave rise to the Baltic amber in the late Eocene or early Oligocene, already show the transition from the piciform to the large type of pit.[1] Conwentz notes that there may be from one to four pits in each cross-field and that the number decreases with the increase in size. He further notes that in certain regions the pits are predominantly small and in others large, but draws no conclusions as to the origin of the latter. From a consideration of the mode of formation of the large ray pits of *Pinus,* we see that the two main divisions of the genus fall roughly into two principal subgroups, one less specialized with one or several small pits in each cross-field of the wood ray and the other more highly specialized with large infrequent pits in thin-walled ray cells. These subgroups grade into one another, but by recourse to other features of anatomical specialization as well as to external characters, a satisfactory basis for further subdivision along true evolutionary lines is obtained.

SUMMARY AND CONCLUSIONS

1. By a study of the anatomy of fossil and living pines certain lines of descent may be somewhat clearly discerned.

2. Cretaceous pines as well as *Prepinus* Jeffrey were

---

[1] Conwentz, Monog. d. Balt. Bernsteinbaeume, pp. 55–56, Tab. XIV, 7, Tab. X, 4.

characterized by thick-walled ray parenchyma and piciform lateral ray pits, by the absence of marginal ray tracheids and by abundant tangential pitting of the autumnal tracheids.

3. The development of ray-tracheids, the disappearance of thick-walled ray cells, the origin of large compound ray pits and the loss of tangential pitting in the autumnal tracheids are all features of the evolutionary development of the pines of the present epoch.

4. The large lateral pits of the rays in modern species of *Pinus* have taken their origin for the most part by the fusion of small pits with distinct circular borders.

5. The hard and soft pines with very large lateral ray pits are the most highly developed living pines. The type of hard pines represented by *P. resinosa* in North America and *P. silvestris* in Europe, represent in the concurrent development of very large generally solitary lateral ray pits, with dentate marginal ray tracheids and the obliteration of tangential pitting in the autumnal tracheids, except in the seedling and in the woody axis of the cone, the most highly developed and specialized condition among living pines.

6. The nut pines of North America and Asia have piciform lateral ray pits and thick-walled ray cells and in these features approach most nearly to the conditions of structure found in Cretaceous pines.

7. The hard pines of the United States, with the exception of *P. resinosa*, show a great range of variation from piciform to compound lateral ray pits. The soft pines present a parallel series of gradation in ray pitting.

In conclusion, I wish to express my thanks to Professor Jeffrey for material of Cretaceous and other pines and for aid in securing the photomicrographs with which this article is illustrated. To Professor Jack I am indebted for specimens of the woods of Asiatic pines and to Mr. E. W. Sinnott for the opportunity of examining serial sections of the seedlings and cone-axes of a number of pines.

FACTS ABOUT THE "LOBSTER PEARL"

PROFESSOR FRANCIS H. HERRICK
WESTERN RESERVE UNIVERSITY

THROUGH the kindness of Dr. H. M. Smith, of the U. S. Bureau of Fisheries my attention was recently called to reports of the discovery of a "lobster pearl," which had a wide circulation in the newspaper press.

In an article credited to the New York *Times,* Mr. Herman Meyer, a pearl dealer in New York, to whom this object had been sent for examination, is reported to have described it as follows:

> As best I can see, the pearl has none of the laminated structure of a pearl produced by a shell. But, while it seems one homogeneous mass, at the same time it is as much a pearl as a lobster can produce, and as true a pearl for a lobster as is a regular pearl for a shell. Lobsters are not in-layers, and the inside meat of a lobster does not move as does the inside of a pearl shell. In my opinion it is a lobster pearl.

In reply to a letter of inquiry on the subject, Mr. Alfred Eno, of Jamaica, New York, gave this account of the finding of the "pearl":

> In July, 1907, accompanied by F. W. Denton, of Hollis, Long Island, I was eating dinner at the Orient Point Inn, Orient Point, L. I., and besides other things, we had some lobsters which had been caught in Plum Gut, off the end of Orient Point, the day before. Mr. Dunton broke open one of the claws of the lobster he was eating, and in biting into the meat, his teeth came in contact with a hard substance

Mr. Eno kept this "hard substance" as a curiosity, and two years later sent it to the dealer in New York, who, as related above, pronounced it to be a true pearl.

The following further details were given to me in a letter by Mr. Meyer:

> The pearl was about 7 millimeters in diameter; nearly round, not smooth; the color was a light manilla, about that of the inside of the shell after boiling. The hardness was about 3; the texture was solid,

without layers, and the fracture was waxy but not brittle nor conchoidal. It had no place where it seemed to be attached to anything, and it had no lustre beyond that of beeswax. To all appearance it seemed the same material as the inside of the claw, without crystalline structure and without layers. Every appearance of the pearl and the manner of the finding, and the two men who found it indicated that it was not a fake. I deal with many of these things, almost daily, and could have determined that fact.

Later through the courtesy of Mr. Eno, I was able to make a careful examination of the so-called "pearl," and to secure the photographs, which are here shown. While my findings, which will be now given in detail, do not support the view expressed above—that we are dealing with a true pearl-like body in any proper sense—they in no way detract from the biological interest of the object, which is without doubt unique.

Description.—The body called a "pearl" is chiefly remarkable for its form, for when seen from one side or pole it has the appearance of a nearly symmetrical sphere, 11 millimeters in diameter (Fig. 1). That it is not in reality regular, but has a long axis at right angles to a flattened side, is better seen by reference to Figs. 2 and 3, in which the object is represented four times its natural size. Its absolute weight is 0.9785 gram.[1] It is of a light buff color, and in all essential respects resembles the shell of any lobster's claw, when seen from the inside, and in the dried state (Fig. 4).

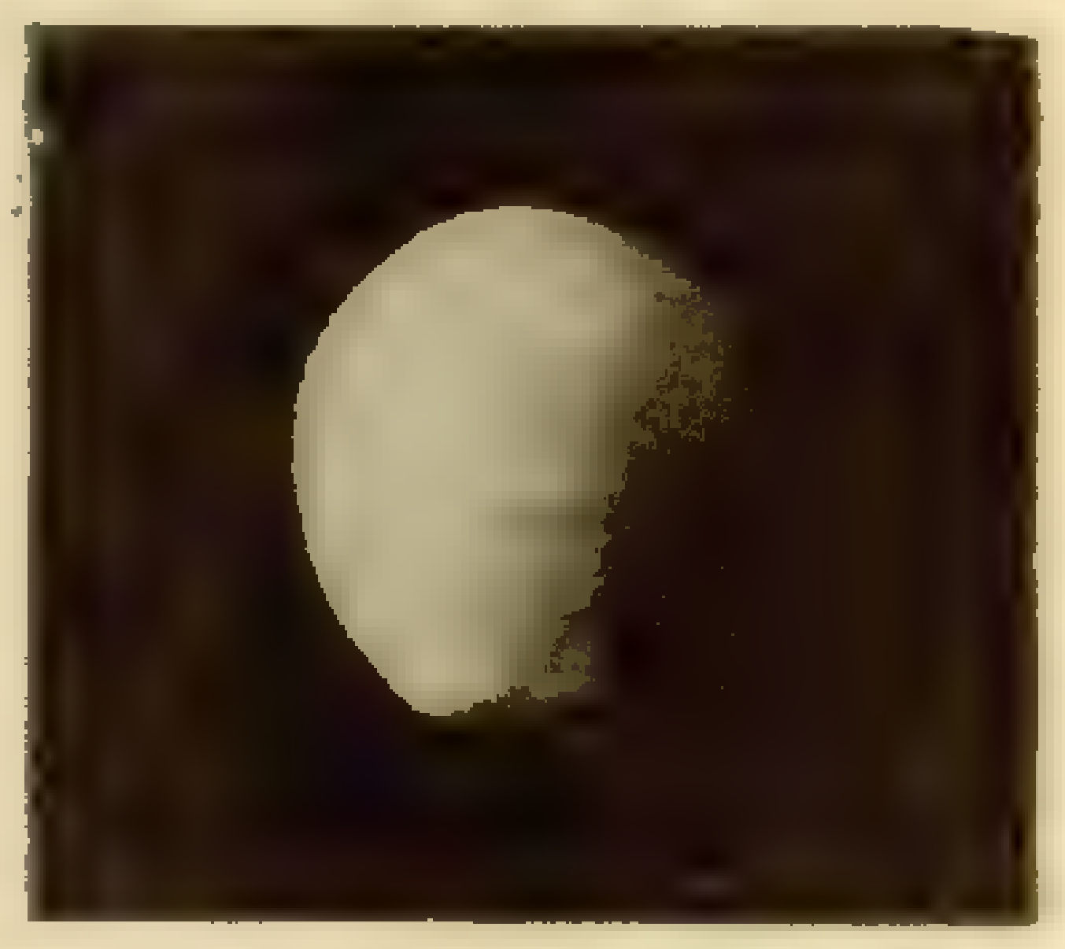


FIG. 1. The "lobster pearl," seen from side parallel with axis of ingrowth. Natural size.

The surface of the body is neither chalky nor waxy, but shines faintly, and has a distinct punctate or granulated appearance. The flattened pole or side, which bears the marks of a knife, and was evidently once rougher than now appears, represents, without any doubt, the original "stalk" or bond of union with the rest of the shell. Close to this base rises a crest one third of an inch long (seen to left of star in Fig. 3), and from this a rather conspicuous furrow diverges and passes diagonally up one side of the mass. In this furrow close to what we regard as the base of attachment, lies a large hair-pore (over star), which is visible to the eye, and into which a needle-point can be easily thrust, while around this base a dozen smaller but quite similar hair-pores can be readily detected with a magnifying glass.

---

[1] For this determination, as well as for the specific gravity of the "pearl," and shell of the lobster's claw, I am indebted to my friend Professor H. W. Springsteen, of Western Reserve University.

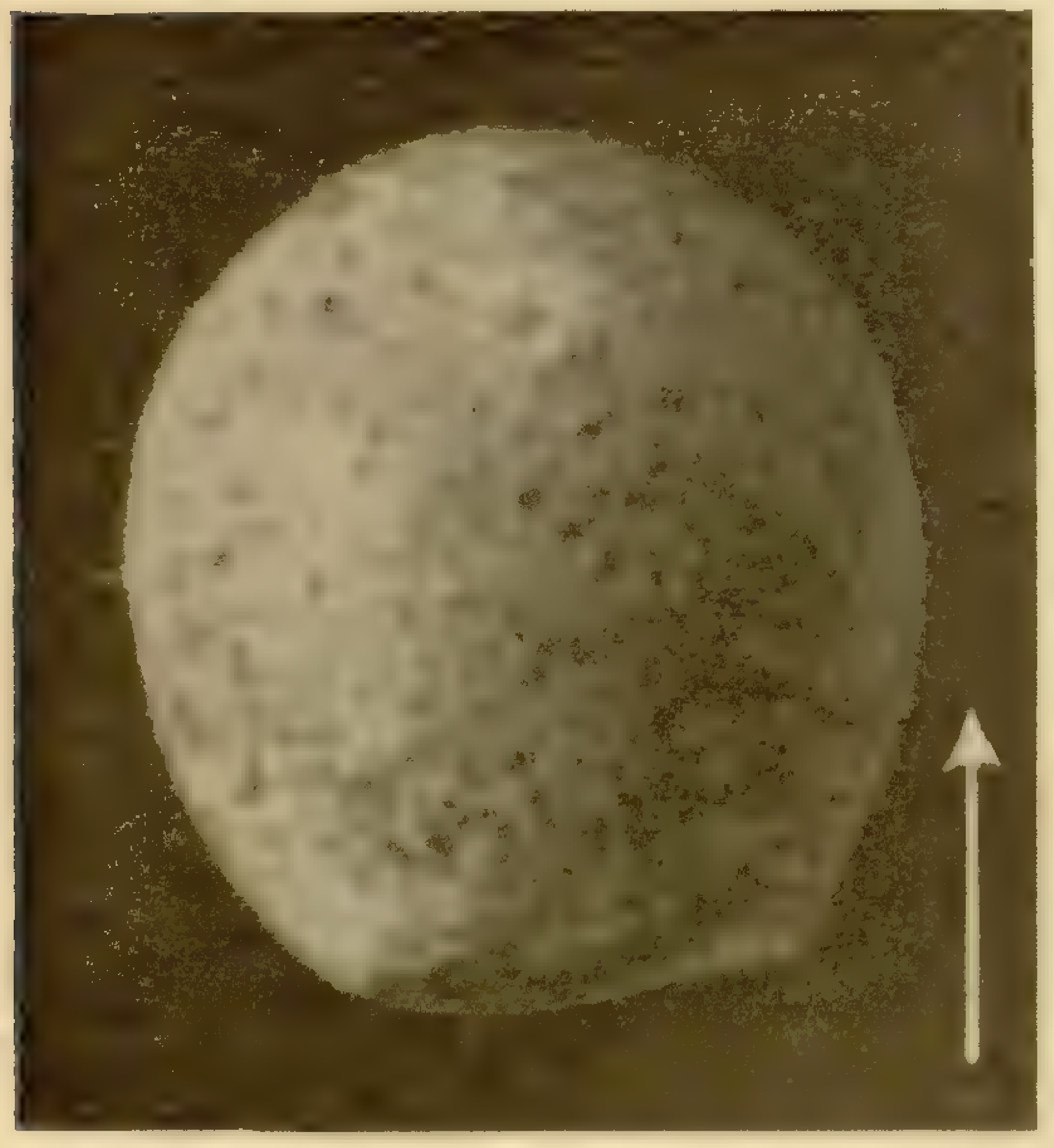


FIG. 2. Sphere, seen from same side shown in Fig. 1, showing elevations corresponding to the tegumental glands. Arrow marks the direction of the ingrowth. Four times natural size.

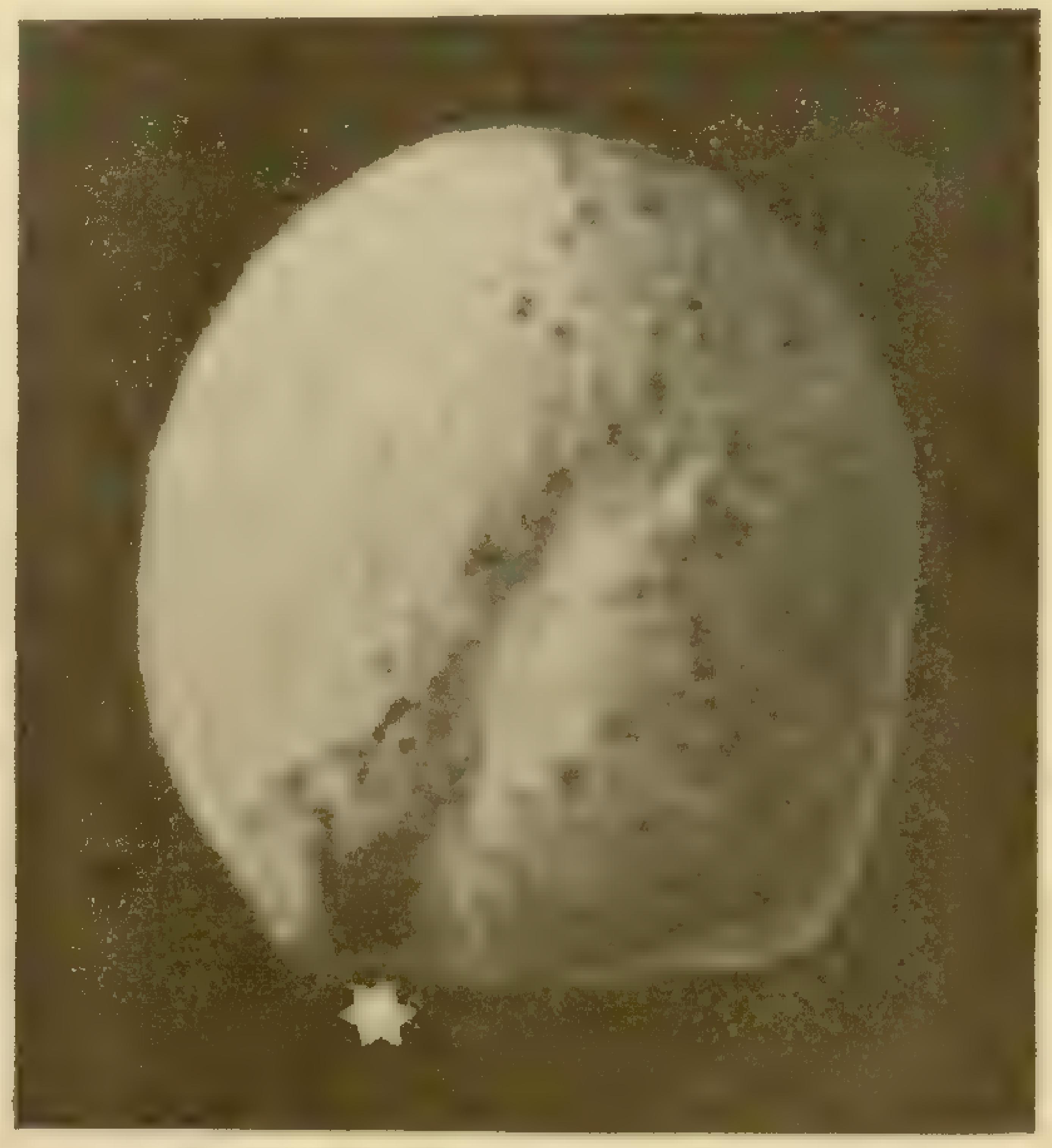


FIG. 3. Sphere, seen from the side opposite that presented in Fig. 2, showing an oblique groove running up from the base of attachment. Large hair-pore near the base is over the star.

The punctuate or granulated surface of the body (Figs. 2 and 3) is seen upon microscopical examination to be due to minute elevations, which are thickly and rather uniformily distributed. Each of these elevations is crater-like, having what appears like a central pore, from which radiate very fine creases or striæ.

The shell of the lobster, although apparently a solid armor, is very sensitive, for it is virtually a strainer, being penetrated in its every part with multitudes of minute vertical canals, which give passage to either sense-organs (sensory setæ, bristles or "hairs"), or to glands (ducts of the tegumentary glands), and thus put the soft and sensitive skin in direct relation to its outer environment. The pores of the tegumental glands open on crater-like elevations similar to those described above, but lie far below the limits of visibility to the naked eye. These glands themselves are usually not over .15 millimeter in longest diameter, and while the length of their ducts is not commonly more than .15 mm., plus the thickness of the shell at that point, their diameter is only .008 mm. The hair-pores, on the other hand, are sometimes visible, being .15 mm. in diameter or larger, while many are much smaller than this, and when the shell from the under side of the big claws is seen from the inside, they are found at the summit of large blister-like elevations (Fig. 4), though too small to show in the photograph. In other places, as in the shell from the upper side of the big claws, the pores of

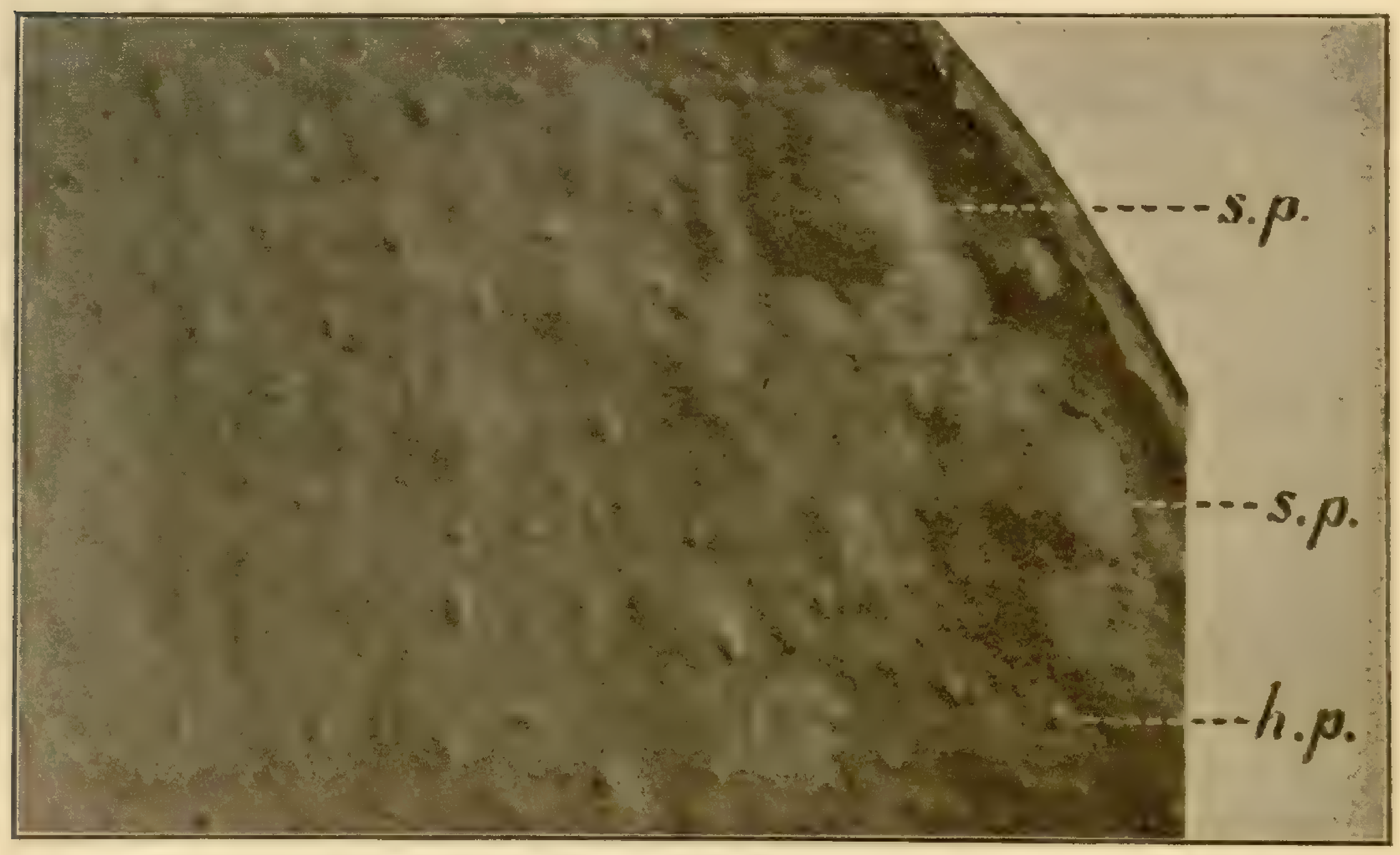


Fig. 4. Photograph of the inner surface of the shell, from the lower side of the toothed claw, showing "blisters" (*h. p.*), which represent the hair-pores. The larger elevated areas (*s. p.*) near the margin are sieve-plates, which give passage to hundreds of setæ. Four times natural size.

this type usually lie at the bottom of corresponding depressions. We consider that the minute elevations on the surface of the so-called pearl mark the positions of tegumental glands, the only other possible conclusion being that they represent extremely minute and no longer functional hair-pores. In any case they prove that the structure of this body tallies with that of the rest of the shell.

It may be added that between the conspicuous "craters" of the more prominent and functional hair-pores (on the inner surface of the shell of the big toothed claw), innumerable smaller granulations occur which do not appear to belong to functional setæ or to glands, while along the lower outer margin of this claw, where the setæ are bunched, each elevated area has the appearance of a sieve, bearing hundreds of holes. Two of these areas, which correspond to very marked depressions on the outside of the shell appear at the upper right hand side of Fig. 4 (*s. p.*), close to the outer margin of the toothed claw, and near its tip. The magnification, however, is not sufficient to show the pore-canals. The hard shell of the lobster is further vertically striated and horizontally laminated, and the same laminated structure can be seen at the base of the body in question, where a knife has been applied.

The specific gravity of the sphere was found to be 1.45, and that of a part of the dried shell of a toothed claw (from upper surface of propodus, near the hinge-joint of a large hard-shelled individual) was 1.43.

It is thus evident that in color, texture, structure and specific gravity, the body under analysis agrees with the shell, being peculiar only in its form, and in the position which it occupied in the meat of the claw. It is not a "pearl" in any sense, but an integral part of the shell, to which it was joined at its short stem or base, until the claw was broken open by the finder.

Origin.—It is safe to say that no proper pearl can be formed in a crustacean, and presumably in no other arthropod, since the hard shell is a differentiated portion of the outer ends of the epithelial cells themselves and in direct organic connection with them, except under the peculiar conditions which determine the molt. The shell of a pearl-secreting mollusk, on the other hand, is a true secretion product, to which deposits are successively made by epithelial cells having a different relation to the shell, which is never cast off. Assuming that a foreign body could by any means find lodgment between the hard and soft parts of a lobster's skin, it would not be free to move as is the case with a grain of sand inserted beneath the mantle of a bivalve mollusk, and if it did not immediately set up a process of regeneration at the point of lesion, the foreign body would be surely lost at the succeeding molt.

If the shell of the claw to which this spherical body pertained had been preserved, its origin could have been traced with greater certainty, but all things considered, it seems to be a vagary of the process of regeneration, due in all probability to some peculiar injury, leading to an ingrowth or pocketing of the skin at that point, instead of to the usual protuberance. It represents a permanent ingrowth of a part of the shell, started in all probability when this was soft, and not later smoothed out or effaced at any subsequent molt. While it would be impossible to prove that this body was not formed, as we see it, during the interval between two molts, it seems quite possible that it has survived more than one casting of the shell, in which case we should have a succession of "pearls," similar to this one, but probably forming a progressive series as regards their size and solidity.

A cruder suggestion would be that this sphere represents one of the grinding tubercles or "molar teeth" of the crusher claw, like the large proximal and usually symmetrical tubercle of the dactyle, pressed into the meat of the claw in some unaccountable manner, and not later restored to a normal condition. The presence of tegumental glands, assuming that these have been correctly identified in the body in question, might lend some support to this idea, for the tubercles are formed by fusion of the sharp teeth, near the apex of each of which a tegumental gland is seen to open, up to the fourth and to even later stages of development before the adult types of claw have been differentiated. I am inclined, however, to regard the body as the result of regeneration, due to injury, in the way suggested above.

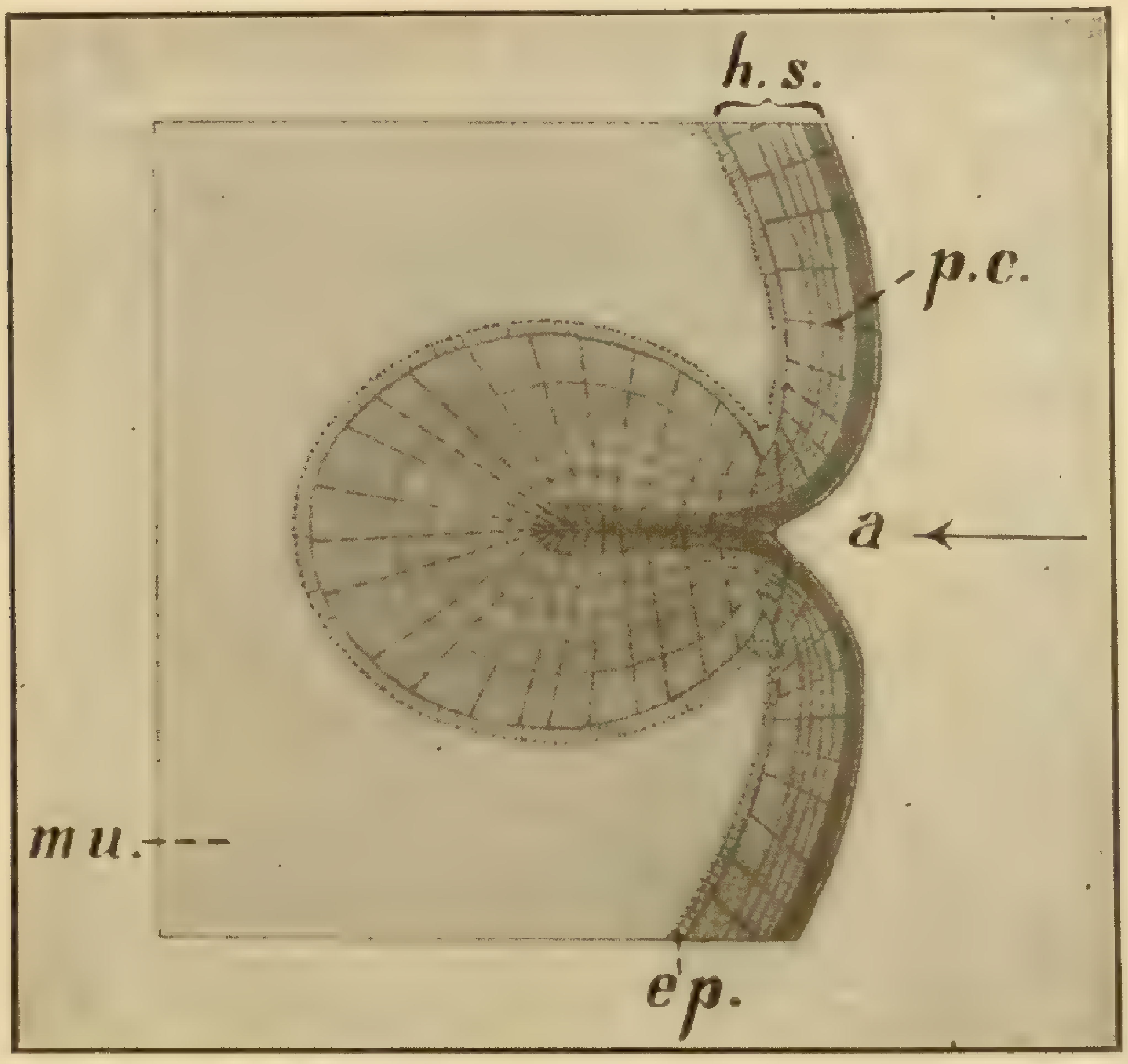


FIG. 5. Diagram to illustrate the origin of the "lobster pearl," the axis of ingrowth being marked by arrow. The horizontal laminæ of the shell, and the vertical canals (hair-pores or capillary ducts of the tegumental glands) being only roughly indicated; *a*, area of ingrowth; *ep*, chitin-forming epithelium of soft skin; *h. s.*, hard shell; *p. c.*, canals penetrating shell; *mu*, muscles.

Reduced to the simplest expression, the ingrowth and shell proper bore the relations shown in Fig. 5, where the axis of invagination is marked by the arrow. The ingrowth involves in succession the soft skin (dermis and chitin-secretin epithelium), the calcified non-pigmented and pigmented strata, and the thin outer enamel layer of the hard shell, but the superficial area of ingrowth (marked *a*) may be represented here as extended too far below the surface. The relations, however, are the same, whether this pocket is deep or shallow, and no attempt is made to express any possible mechanical conditions which might determine the inward rather than outward direction of such a fold.

SHORTER ARTICLES AND CORRESPONDENCE

AN EIGHTEENTH CENTURY MICROSCOPE[1]

EARLY microscopes are uncommon and our knowledge of the sequence of their forms is in part to be gained by random discoveries. The instrument shown in the figure was obtained recently from the antiquary Meyer in Zürich (who said that it had formed part of the collection of Sir Henry Angst), and it is worthy of comment, both for its early date, and its admirable preservation.

It dates, in all probability, from the early years of the eighteenth century. It resembles in essential regards John Marshall's[2] microscope of about 1700 and Hertel's[3] of 1716. Indeed it may possibly be slightly earlier than the Marshall instrument, for in some regards it is more archaic. Thus it conserves the tripod-shaped support, and lacks the mechanical focusing adjustment. It is, moreover, not an instrument of common class in which such features would be retained at a late date by reason of economy, for its workmanship is throughout precise and elegant. On the other hand, it is furnished with a sub-stage mirror which suggests a transitional form to the Hertel stand. The stage and the supports of the barrel are of brass, as well also as the upper rim of the eyepiece, which is provided with a dust-proof sliding cover, as in early spy-glasses. The barrel and its supporting tube are of carton; the former is covered with green paper which bears rings as guides for focusing, and gilt bands, the latter is decorated with Chinese shagreen. The base of the barrel, the mounting of the objectives and the region of the eyepiece are of ebony. The base of the stand is octagonal, ornamented with moulding and furnished with a drawer for accessories. It is quite similar to the Marshall instrument in this regard, and in the turned supports of the eyepiece and of the objective.

There is but one eyepiece, its lenses measuring 1 inch and 1¾ inches in diameter, and it can not be removed from the stand.

---

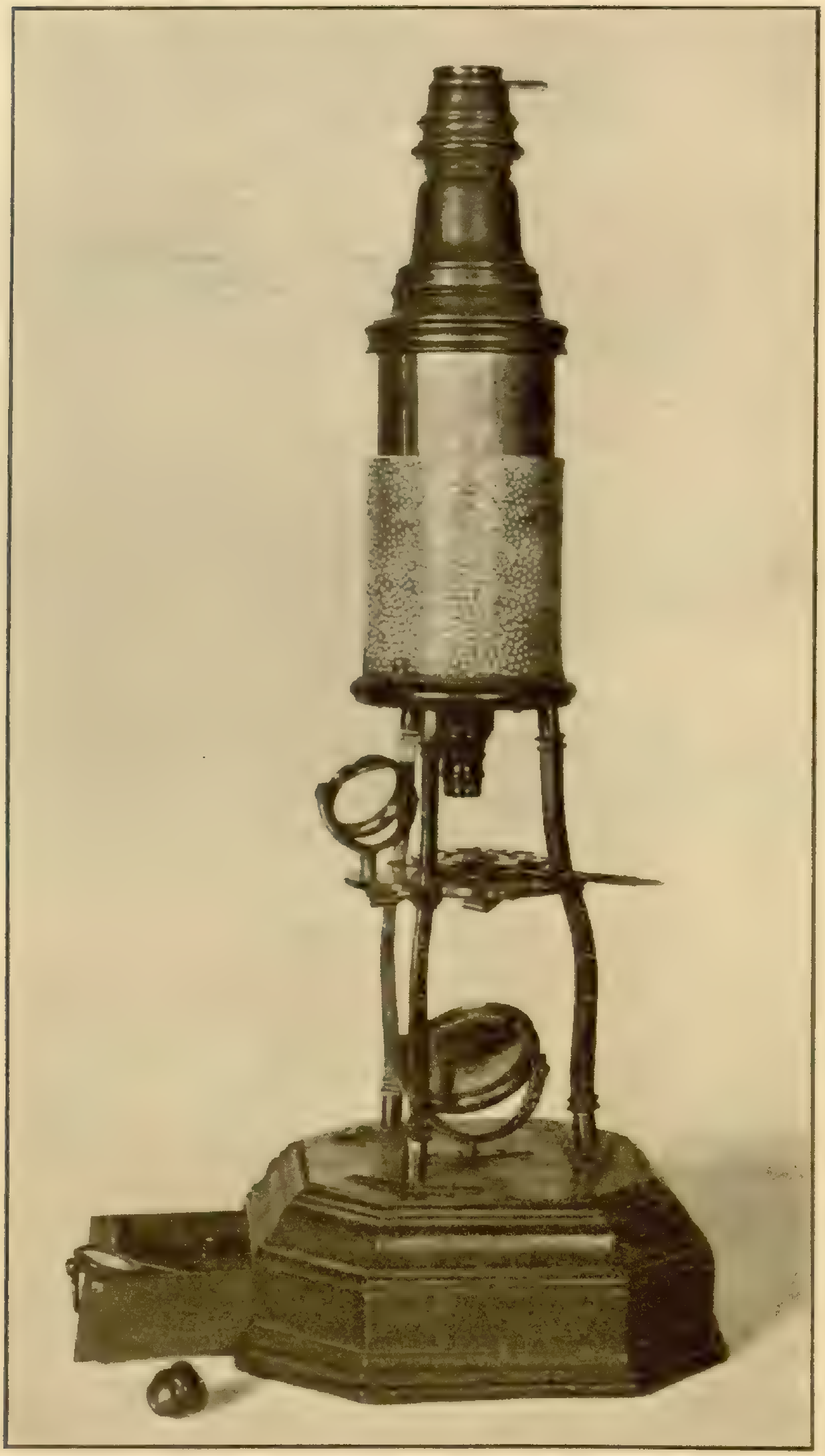
[1] Recently presented to the American Museum of Natural History.

[2] Cf. Harris's "Lexicon Technicum," 1704, and figured by Carpenter (VII. ed.), 1891, p. 136.

[3] *Op. cit.*, pp. 137–138.

There are five objectives, numbered, of which No. 1 is the highest. The power of magnification is as follows:

Eyepiece and objective 5 = 20 diameters (at 10 inches).
Eyepiece and objective 4 = 28 diameters (at 10 inches).
Eyepiece and objective 3 = 50 diameters (at 10 inches).
Eyepiece and objective 2 = (broken)
Eyepiece and objective 1 = 330 diameters (at 10 inches).



The lenses are simple (achromatic doublets dating only from the early nineteenth century) and are diaphragmed extensively.

In fact, the lens of the highest objective is enclosed in a brass capsule which is perforated on either side, the perforations measuring about $\frac{1}{25}$ of an inch in diameter. With the highest power there is an extraordinary working distance—one eighth of an inch. The maximum magnification, by the way, corresponds roughly with that of a modern Leitz microscope, having a No. 6 objective and No. 1 eyepiece.

The accessories include stage-forceps, a small bull's-eye condenser, a hand lens, forceps, extra concave mirror, a long handle (?), a plano-concave lens, and ten objects mounted dry in sockets in a wheel-like carrier. The objects are still in place and include pollen, flea, wing of fly, spider and insect scales.

BASHFORD DEAN.

STOMATOLEPAS, A BARNACLE COMMENSAL IN THE THROAT OF THE LOGGERHEAD TURTLE

While investigating the parasites of the loggerhead, *Caretta caretta,* at the Marine Laboratory of the Carnegie Institution at Tortugas, Florida, Professor Edwin Linton found numerous small barnacles partially imbedded in the mucous membrane of the upper end of the gullet. Many sessile barnacles are known to live externally on marine turtles, whales, etc., but up to this time none has been known living internally.[1] One group of Cirripedia, the Rhizocephala, consists wholly of parasitic forms which penetrate their crustacean hosts through the external integument. The barnacle discovered by Professor Linton which we will call *Stomatolepas,* seems to be the first commensal form of the thoracic cirripedes.

Stomatolepas has about the size and shape of a split pea, the oral surface being flattened. The calcareous walls form a shallow bowl which is imbedded about half of its depth in the membrane of the gullet or posterior part of the mouth of the host.

Stomatolepas prægustator n. sp.

The walls form a very broad, shallow cup, nearly circular in contour, and about twice as wide at the opening as at the base. The base is flat, circular, excessively thin, but sufficiently calcified to be rigid and retain its shape when dried. The plates of the wall are composed of two layers, an inner layer, thin, dense and transparent, and an outer covering of several layers of thin-walled cells. Externally a shallow radial sulcus in the cellular surface marks the sutures between the plates. Each plate has a triangular smooth median area at the base, where the outer cellular layer is lacking, and the arched projecting upper ends of the plates also lack the cellular layer. The summits of the rostral and lateral plates are broader than the bases and strongly arched; the cardinal plate projects less above the cellular layer and is lower than the others. Internally the plates of the wall are glossy, show no sheath, and are transversely ridged, the ridges very narrow, parted by wide smooth intervals and about twelve to fifteen in number: the basal fourth or third of each plate is smooth.

---

[1] The stalked barnacle *Dichelaspis* lives in the gill cavities of crabs, but is not truly parasitic or commensal.

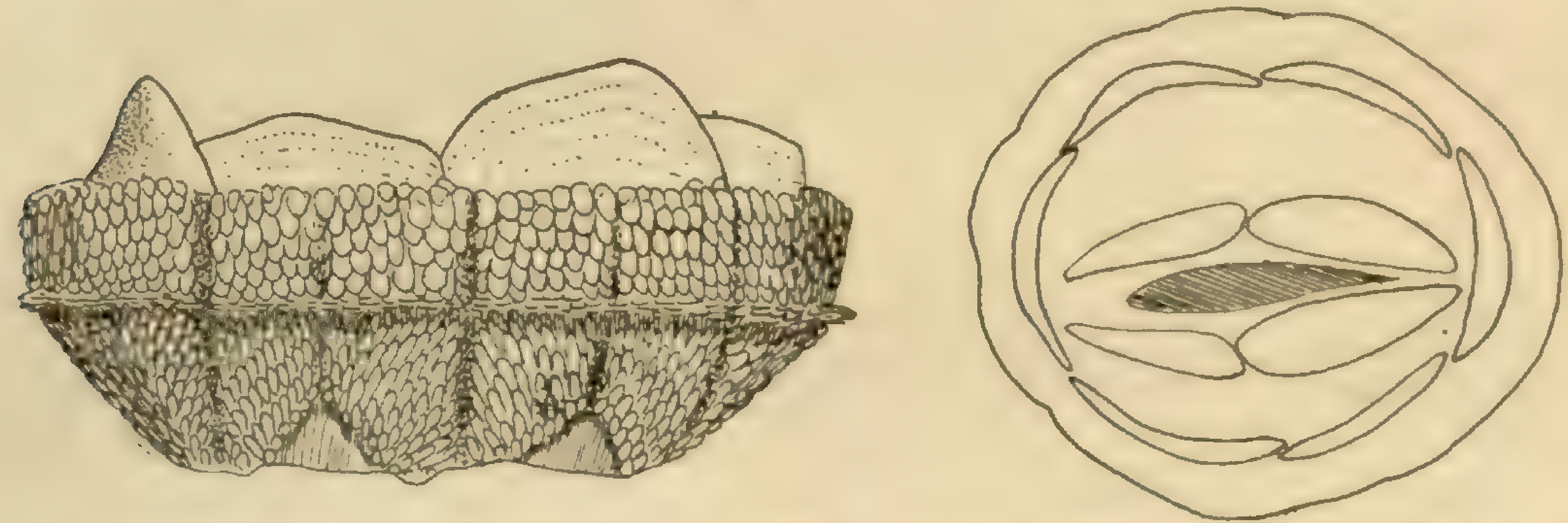


FIG. 1. *Stomatolepas prægustator*, lateral view and diagram of the oral face.

Length of the walls 6.7, diam. 6, height 3 mm.

The opercular plates protect less than half the area of the orifice, are very thin, glossy, white and smooth both outside and within. They are long and narrow, the terga in contact with the scuta but not articulated or interlocking in any way. The scuta are longer than the terga, tapering to a point at the rostral end, rounded at the tergal end.

The cirri are rather short. The first has unequal rami of 8 and 12 segments; the rest have subequal rami, the sixth pair having 20 and 22 segments. The segments are armed with two pairs of long spines, and on some of the median segments a third extremely minute pair. Posteriorly there is a pair of small spines at the distal angle of each segment.

The penis is about as long as the cirri, very densely annulate, bearing very few minute hairs. There is a dense terminal pencil of very short hairs.

The mandible has four large spines and a blunt, multispinose lower angle. The maxilla has two large spines above followed by a small notch, below which there are 7 to 10 spines.

Stomatolepas belongs by its non-articulated scutum and tergum to the subfamily Coronulinæ as defined by Gruvel,[2] being most closely related to the genera *Tubicinella* Lam., which lives on the skin of whales, and *Stephanolepas* Fischer, a barnacle which lives imbedded in the plates of *Thalassochelys imbricata.* Both of these have the wall more or less tubular and conspicuously annulated externally. In *Stomatolepas* the wall is depressed and broadly bowl-shaped, and covered externally with a mass of thin-walled cells.

Henry A. Pilsbry.

THE AGE OF SPEED SIRES

The contribution by Professor F. R. Marshall in The American Naturalist for January, 1909, on the age of speed sires, escaped my notice until recently called to my attention. In that article Professor Marshall refers to the fact that I found the average age of trotting sires to be 10.43 years, and that by taking all sires in four generations of ancestors of 2:10 trotters I found the average age at approximately 14 years.

Professor Marshall objects to this comparison as not being a fair one on the ground that by going back four generations from our 2:10 trotters we go back into the formative period of the breed. This formative period, he asserts, followed the descent from Hambletonian 10, foaled in 1849, and involved his sons, which were used largely in the stud until old age. This he holds produced an abnormal number of old sires at that period of history, and that by including them in my tables I was drawing unwarranted conclusions from what was a mere incident. This he reinforces by showing that the *immediate* sires of 242 trotters in the 2:10 list were of the same age that I found for the normal breeding age of 1,000 cases.

In this matter Professor Marshall labors under a misapprehension. The average age of 10.43 years for sires which I found was the average as it existed in the "formative period" from 1840 to 1890. The "Register" from which they were taken was published in 1892 and contained an alphabetical list of all standard horses from the earliest date up to immediately before 1892. The tabulation was taken alphabetically from the index and the 10.43 is an accurate representation of what occurred when the grandsires, great-grandsires and great-great-grandsires of our 2:10 trotters were living and being bred.

There is, in this matter, food for profound thought, and, without being too accurate in decimals, I will briefly state the situation as it exists. The immediate sires of our 2:10 trotters are of an average age of 10.4 years. The grandsires are the immediate sires of the sires and dams of 2:10 trotters, and as immediate sires they should be 10.4 years of age, which was the average age of sires at the time they became sires in these pedigrees. But they are not. In these pedigrees they are 12.5 years of age. Evidently something has happened to disturb the normal conditions.

---

[2] "Monographie des Cirrhipèdes on Thécostracés," pp. 9, 270.

Again, the great-grandsires were the immediate sires of the grandsires, and they became such when the Hambletonian family was breeding at 10.4 years between generations. But they did not become sires in these pedigrees at their own average age at reproduction, but at 13.5 years. Going back one more generation in these pedigrees we find the sires to be 14.5 years, going another generation we find them at 15 years, and going still another generation we find a total of 467 horses being sires at an average age of 15.98 years!

Certainly, no one in his senses will believe that horses were ever bred in this or any other country at such average ages as these for any considerable body of them. Something extraordinary has occurred, and that something deserves careful thought and a reasonable explanation. That this matter is really extraordinary I will illustrate by calling attention to another feature. Some of the horses which appear as sires in the different generations were sent to the race track, while others were never raced. When a horse is raced, he spends his early years on the race track and is retired to the stud after his racing career is over. As a consequence, of two brothers, one of which went to the track and the other of which went directly to the stud, the one which is raced becomes a sire at the higher average age, and they should appear so in these pedigrees. But they do not. The ages previously given are the ages of the sires which had no standard records. The sires with records which appear in these pedigrees appear in each and every generation at an average age of less than 10 years.

Now, why is this? No reference to a formative period is an explanation when both kinds of horses were living and breeding at the same time. In the best pedigrees, those horses which had standard records appear at less than the average breeding age, while those which had no records appear at about four years above the average breeding age. CASPER L. REDFIELD.

NOTES AND LITERATURE

BIOMETRICS

Recent Quantitative Studies on Variation in Social Insects.—The social insects (ants, bees, wasps and termites) because of the differentiation of their populations into "castes," distinguishable from one another in somatic characters, present a whole series of interesting problems in variation, heredity and morphogenesis. These animals afford very alluring material with which to undertake biometrical study of various problems within the fields mentioned. It is a matter of comparative ease to get relatively large numbers of individuals. The firm exoskeleton makes measurement, and the preservation of material unchanged for future measurement, comparatively easy. Finally, in addition to the wide variety of somatic structure to be found in the several castes, the relation of these castes to sexual and asexual modes of reproduction also adds to the intrinsic biological interest and usefulness of the material for the study of general problems.

In view of these considerations it is somewhat surprising that more biometric work has not been done with the social insects as material. So far as the writer is aware there has as yet been but one quantitative study of variation in ants, that of Kellogg and Bell (10). With bees the case is somewhat better. Here we have, besides the earlier work of Koschewnikow (11, 12) and Bachmetjew (1, 2, 3, 4, 5 and 6) the careful quantitative studies of Casteel and Phillips (7), Kellogg and Bell (*loc. cit.*) and Kellogg (9). Miss Entemann's (8) study of variation in the coloration of *Polistes,* which was quantitative in character, was the only study of the kind on wasps before 1907.

During the last two years two papers dealing with variation in wasps have been published from Pearson's Biometric Laboratory. The first of these, by Wright, Lee and Pearson (16), deals with the results of a study of the variation exhibited by the individuals of the several castes (queens, drones and workers) taken from a single nest of *Vespa vulgaris.* From the material contained in this nest it was possible to get measurements of 129 queens, 130 drones and 129 workers. The length and greatest breadth of each wing were measured, as well as the dimensions of various "cells" marked off by the wing veins. Altogether seven absolute measurements were made and from these six indices were calculated. The first point brought out by the measurements is that the wings of queens are larger than those of drones, and the drones in turn possess larger wings than the workers. There are some differences in the proportions of the wings in the three castes, though these differences are not relatively so great as those in absolute size. There are only slight differences, either in absolute size or proportions, between the wings of the two sides of the body. All these are facts easily enough ascertainable by direct observation. The biometrical expression makes more precise and accurate what was already known. In regard to the absolute size of the wing the worker is absolutely and relatively more variable than the drone, and the drone than the queen. In regard to the proportions of the wing (as measured by the indices) this relation is nearly reversed, though the differences are much smaller; the drone is slightly less variable than the worker, and the queen is less variable than either. The degree of relative variability, as measured by the coefficient of variation, is exceedingly small for some of the dimensions of the wasp's wing. The mean coefficients for queens' wings are for absolute dimensions 1.57 (right wing) and 1.54 (left wing) and for indices 1.28 (right wing) and 1.25 (left wing). These are among the smallest variabilities yet recorded.

The highest correlations between wing dimensions were found in the workers, and (with the exception of a single pair of characters) the lowest correlations in the queens, the drones taking an intermediate position. The index correlations were found to be nearly all negligibly small. On the basis of this result the suggestion is made that these wing proportions, as given in the indices, ought to be useful taxonomic characters.

The point of greatest interest brought out by this first study of wasp variation is the relative variability exhibited in the different castes, as compared with what has been found for bees. There can be no doubt apparently that in bees the drones are *more* variable than the workers. This result was announced on rather dubious statistical grounds by Casteel and Phillips (7), criticized by Lutz (13), but abundantly confirmed by Kellogg (9) and by Pearson's (16, p. 422) reductions of the data of Casteel and Phillips. In the wasp the drones are distinctly *less* variable than the workers.

A second study of variation in wasps already referred to has appeared quite recently. The work was done by Thomson, Bell and Pearson (14) and deals with the comparative variability of queens taken from a single nest, on the one hand, and of an equally large sample of queens, presumably taken at random from the "general population" of queens, on the other hand. Such a comparison is obviously of a great deal of interest biologically. First as to the source of material for the study: The queens from a single nest were the same ones that were used in the first study discussed above. The "general population" queens were obtained in the following way:

> The queens for this second investigation were obtained in the spring of 1908 in the neighborhood of Gerard's Cross. As soon as the first queen wasp appeared, a reward of 1 *d.* was offered for each queen wasp brought, and considerably over 200 were then rapidly collected. . . . The specimens came in small numbers, sometimes one at a time, often alive, and there is no reason to doubt that they represent a genuine sample of the queen wasps of the autumn of 1907, which survived the winter and were starting in the spring of 1908 to establish their nests.

This "general population" material collected in the way described would appear to be open to serious criticism from several points of view. In the first place, as pointed out by the authors, these "general population" queens represent a different locality and season of the year from the single nest queens with which they are compared. Nothing is known about the effect of environmental and seasonal influences upon the characters studied. In the second place, it is difficult to find in the sentences quoted above, which is all the information that is offered touching the point, any real concrete evidence that these queens collected on the bounty system really were, as a matter of fact, a truly random sample of the "general population" of queen wasps. Since they all came from one restricted locality more than a suspicion is raised, considering the habits of wasps and the relative frequency and distribution of wasp nests, that they may all have emanated from a very few original nests. If they did the whole paper is vitiated. It is not of course meant to assert that they *did* come from a few nests only, but it is desired merely to point out that the authors of the paper apparently have no evidence (and made no attempt to get any) that they *did not* so originate. It might be held that the values of the biometric constants calculated for these queens constitute evidence that they are a random sample of the general population. But this is merely arguing in a circle. It is precisely equivalent to saying that two and two make four *because* four is made by two and two. The constants are, in the first instance, calculated and their values are subsequently used in the discussion on the assumption that the material is really a random sample of the general population. The discussion of the biological import of the constants has no significance if this assumption is not true. This being so, it is not feasible to turn around and say that the values of the constants prove the randomness of the material.

On the basis of this rather dubious material the discussion of a very interesting question of inheritance is undertaken. The characters dealt with are the same as those of the former paper. The first point brought out is that there is a slight but definite differentiation between the "single nest" and the "general population" queens. The authors state that they are not clear as to what is the cause of the differentiation. The main point of the paper turns on the relative variability of the two groups. Taking first the standard deviations (the coefficients of variation show the same thing), it appears that the "single nest" queens are roughly only just about half as variable as the "general population" queens. A long discussion follows regarding the question of whether the amount of this reduction in variability in the single nest is what would be expected on the basis of the law of ancestral inheritance. The general outcome is that it is not! There are, however, so many biological factors about which the authors avowedly have no data at all, concerned in the production and interpretation of the observed results, to say nothing of the general difficulty about the randomness of the "general population" sample, that the discussion fails to be very convincing in any direction. This particular case well illustrates a tendency which seems likely to do a good deal of harm to the biometrical cause, so far, at least, as biologists are concerned. The whole discussion of inheritance in wasps in this paper rests on a series of premises and assumptions regarding wasp *biology,* which are made without any attempt whatever first to learn by direct investigation the actual biological facts. This method of developing a long and involved theoretical argument, with very far-reaching ultimate conclusions, upon an exceedingly slender basis of facts, gives such discussions of heredity a highly academic, not to say Pickwickian, flavor. In general one can not help feeling that if one becomes seized of a desire to know how characters are inherited in wasps the direct and straightforward way to set about easing his intellectual pangs is to breed wasps under controlled experimental conditions and observe the results. The technical difficulties of dealing with this particular material in this way would doubtless be considerable, but probably not absolutely insurmountable. In any event it would seem that indirect methods of studying inheritance should be only a sort of last resort when direct methods have failed or can not be applied.

The correlations are also found to be reduced in the nest as compared with the "general" population. The amount of this reduction is shown to be that which would be expected as a statistical consequence of the observed reduction in variability of the one population compared with the other.

Warren's (15) termite paper contains a wealth of interesting biological data. It presents the constants calculated from a very extensive series of measurements of the character head breadth in the different castes of several species of South African termites. The bulk of the data are from one species, *Termes natalensis.* A typical nest of this species contains the following kinds of individuals: (1) A single king and a single queen, these being the only sexually mature forms present; (2) soldiers of two sizes, asexual; (3) workers of two sizes, asexual; (4) winged males and females, not sexually mature; (5) young or immature members of castes (2), (3) and (4). Some of the more interesting results which come out of this work are as follows:

There is considerable seasonal variation in the individuals of the same nest. The mean is smallest and the absolute variability greatest in material taken in November, and the mean is greatest and the absolute variability least in March material. Warren offers the following explanation of this result:

> This seasonal variation probably arises from two causes at least: (1) the elimination of the physically unfit, (2) post- "adult" growth. With reference to the first cause it may be noticed that it is very probable that more individuals arrive at maturity from August to November, that is during the first rains, than at other seasons, and therefore the stunted adults will be more abundant during this period, with the result that the mean would be lowered and the standard deviation would be raised. By the time that March arrives the small and weakly individuals of the nest are likely to have died, and consequently the mean will be raised and the standard deviation will be diminished. The second, and perhaps more potent influence, is that the so-called "adults" appear to grow to a certain extent even after their exoskeleton has become hard and yellow.

The workers of *T. natalensis* are on the average less variable than the soldiers. The ratio of worker variability to soldier variability is about 0.8. The sexual castes are less variable than the asexual, both in *T. natalensis* and as an average of the study of other species of termites. The variability of a "general population" of *T. natalensis* obtained by adding together random samples of 100 individuals each (the small soldiers being the caste chosen) from 30 different nests. The coefficient of variability obtained from this population was 7.02 as compared with 3.02 as the average coefficient for single families (*i. e.*, nests). There is thus a reduction here, as in the wasps, of about 50 per cent. in variability in passing from "general population" to single nest. The "inter-nest" correlation of the means between any two castes is about 0.9. The author points out that:

> It is curious that the correlation between similar castes (large and small soldiers) does not appear to be greater than that between dissimilar castes (small soldiers and large workers).

From a study of the correlation between the coefficients of variation it appears that:

> In any given nest when one caste happens, say, to be particularly variable, it does not follow that every other caste is correspondingly variable. From *a priori* reasons one would have expected that the variability of the different castes in a nest would have been closely related, if the variability is to be regarded as an inherited character. If, on the other hand, the variability is to be mainly referred to nurture or to the general environmental conditions, the above results are intelligible.

Bachmetjew (5, 6) has developed an intricate and highly organized theory regarding the existence and origin of polymorphism in the normal bee colony. This theory is supposed by its author to rest upon a solid "statistisch-analytische" foundation. In reality this statistical "foundation" is of such character as to make one wonder at times whether the author (by training a physicist and presumably familiar through that discipline with the elementary principles at least of the mathematical theory of probability) is really serious, or whether he is not perpetrating a great biometric practical joke. The character with which Bachmetjew has dealt in bees is the number of hooks on the anterior margin of the posterior wings. His central thesis, which he at once proves (?) and then forthwith applies to aid in still greater biologico-metrical onslaughts, is to the effect that if a group of individuals (size of group not specified and apparently not regarded as in any way important) shows *two* observed maxima of frequency, with respect to a character expressed in integral or discrete units (*e. g.*, hook number), then the eggs (or seeds) from which the individuals of the group originated were fertilized. If, on the other hand, but *one* maximum of frequency is to be observed, then the individuals developed parthenogenetically. This neat, though somewhat far-reaching, generalization, rests solely and simply on the location by *inspection* alone of modes or maxima of frequency in samples of from about 50 to 150 individuals! Nowhere in Bachmetjew's papers is there any indication of such a concept as that the observed frequencies might have a probable error ever having disturbed the placid progress of the reasoning.

To give these comments point some of Bachmetjew's frequency distributions may be examined. Here are some distributions *supposed* (with a mathematical naïveté probably nowhere to be paralleled in scientific literature) to show two maxima of frequency at the points indicated by the bold faced type (Bachmetjew (5)).

A. (p. 6)	B. (p. 7)	C. (p. 7)	D. (p. 9)
1	1	1	2
2	1	9	5
9	7	11	13
11	**28**	**27**	**19**
21	**31**	**27**	15
21	18	22	**15**
21	9	9	11
16	2	2	80
5	2	2	
2	99	110	
1			
110			

It certainly demands the most consummate scientific insight to discern why the two modes in A and C, for example, should be located as they are. And again the unenlightened statistician wonders what it is about the second 15 in D which makes it a mode rather than the first 15. Is it possessed of a different essence or *aura*, say a sort of transcendental "fifteenness"?

Or again, to take but one more example, who would have supposed that distribution E had two modes while F had but one? (Bachmetjew (5)).

E. (p. 8)	F. (p. 19)
2	1
5	1
10	1
22	4
24	8
17	14

12	15
8	18
100	20
	10
	4
	4
	100

This is indeed esoteric biometry! So much so that it seems hardly advisable to review the theoretical considerations which are made to flow from the sort of statistics presented.

Literature Cited

1. Bachmetjew, P. Ein Versuch, die Frage über die Parthenogenese der Drohnen mittels der analytisch-statistischen Methode zu lösen. Allg. Zeitschr. für Entomol., Bd. VIII, Nr. 2–3, pp. 37–44.
2. ——— Eine neue Methode zur Lösung der Frage über die Parthogenese bei Drohnen. Russische Bienenzucht-Liste, Bd. VIII, Nr. 1. Moskau, 1903. (In Russian.)
3. ——— Der Unterschied der sogenannten falschen Drohnen von den gewöhnlichen, betrachtet vom Standpunkt der analytisch-statistischen Methode aus. Russische Bienenzucht-Liste, Bd. IX, Nr. 4. Moskau, 1904. (In Russian.) Also published in German in Insekt.-Börse, Bd. XXI, No. 47, pp. 371–372. 1904.
4. ——— Ein Versuch, Dzierzon mit Dickel zu versöhnen. Zeitschr. für Naturw. und Geograph., Nr. 4 and 5. Moskau, 1904. (In Russian.)
5. ——— Analytisch-statistische Untersuchungen über die Anzahl der Flügelhaken bei Bienen und die daraus hervorgehenden Konsequenzen. Zeitschr. für wiss. Zool., Bd. XCIV, pp. 1–80, 1909.
6. ——— Die statistisch-analytische Methode im Dienste der Bienenkunde. (Hym.) Deutsch. Entom. Zeitschr., 1910, pp. 15–22.
7. Casteel, D. B., and Phillips, E. F. Comparative Variability of Drones and Workers of the Honey Bee. Biol. Bulletin, Vol. VI, pp. 18–37, 1903.
8. ——— Enteman, Wilhelmine M. Coloration in Polistes. Carnegie Institution of Washington, Publ. No. 19, 88 pp. 1904.
9. ——— Kellogg, V. L. Variation in Parthenogenetic Insects. Science, N. S., Vol. XXIV, No. 622, pp. 695–699, 1906.
10. ——— Kellogg, V. L., and Bell, R. G. Studies of Variation in Insects. Proc. Wash. Acad. Sci., Vol. VI, pp. 203–332, 1904.
11. Koschewinikow, G. Materialien zur Naturgeschichte der Biene (Apis mellifica L.).—Nachricht. der Kais. Gesellsch. der Liebhaber der Naturw., Anthropol., und Ethnogr., Bd. XCIX; Arbeit. der Zool. Abth., Bd. XIV, 1 Lief. (144 pp.) Moskau, 1900. (In Russian: cited after Bachmetjew.)
12. ——— Materialien zu der Naturgeschichte der Biene (Apis mellifica L.) 2 Lieferung. Ueber den Polymorphismus bei Bienen und anderen Insekten. Ibid., Bd. XIV, 181 pp. Moskau, 1905. (In Russian; an abstract has been published by Bachmetjew in Zeitsch. f. wiss. Insektenbiol. Bd. V, p. 246, 1909.)
13. Lutz, F. E. Variation in Bees. Biol. Bulletin, Vol. VI, pp. 217–219, 1904.

14. Thomson, E. Y., Bell, J., and Pearson, K. A Second Coöperative Study of *Vespa vulgaris.* Comparison of Queens of a Single Nest and Queens of a General Population. Biometrika, Vol. VII, pp. 49–63, 1909.
15. Warren, E. Some Statistical Observations on Termites, mainly based on the Work of the Late Mr. G. D. Haviland. Biometrika, Vol. VI, pp. 329–347, 1909.
16. Wright, A., Lee, A., and Pearson, K. A Coöperative Study of Queens, Drones, and Workers in Vespa vulgaris. Biometrika, Vol. V, pp. 407–422, Pl. XXII, 1907.

RAYMOND PEARL.

EXPERIMENTAL ZOOLOGY

The Effects of Extirpation and of Transplantation of the Reproductive Organs in Insects.—Meisenheimer[1] has carried on extensive experiments with moths for the purpose of determining whether the differentiation of the accessory genital organs and of secondary sexual characters is dependent on the ovary and testis or whether their development is independent of the sex glands. The material used was chiefly the moth *Lymantria* (*Oeneria*) *dispar* L., which has a marked sexual dimorphism and recovers well from the effects of operation. The caterpillar passes through five moults before pupation, the first moult taking place about five days after hatching, and each later one in from eight to twelve days, according to temperature; pupation takes place in about six days after the last moult and lasts for three or four weeks. The operations consisted of removal of sex glands, removal of anlage of accessory genital apparatus, transplantation of sex gland of the opposite sex, and removal of wing anlage. The operations were done on all six caterpillar stages, the extirpation of sex glands being done by means of an electric needle in the first two stages, and by a knife in later stages. The mortality was very great, only 51 caterpillars surviving the electrical operation out of 1,250, and 176 out of 537 surviving when the organ was cut out.

In moths from caterpillars whose testes had been removed, the vasa deferentia ended blindly; otherwise the accessory sexual apparatus was perfectly normal. In one case, the vasa deferentia had fused at their free ends, owing to their proximity at the time of healing. The secondary sexual characters, such as the size, coloring and markings of the wings, were of the normal male type. When, in addition to castration, the anlage of the accessory sexual organs, including the vesiculæ seminales, ductus ejaculatorius, penis and most of the vasa deferentia, was removed, there was no trace of these organs in the moth; all that remained of the sex apparatus was a rudiment of the vas deferens on each side and the chitinous supports of the copulatory apparatus whose anlage had not been removed. To make sure that the lack of the accessory organs was not influenced by the absence of the testes, some experiments were done in which the testes were left intact and merely the anlage of the accessory organs was removed. As a result, moths were obtained whose testes were normal and the short ducts leading from them filled with mature sperm, but none of the accessory apparatus was present whose anlage had been removed. There was no influence on the secondary sexual characters when castration was followed by removal of the anlage of the accessory organs.

---

[1] Experimentelle Studien zur Soma- und Geschlechts-Differenzierung.'' Erster Beitrag. Von Prof. Johannes Meisenheimer. Jena, Gustav Fischer, 1909.

In moths whose ovaries had been removed there was usually no effect on the accessory sexual organs or on the secondary sexual characters. Sometimes, however, there was a slight effect on parts of the accessory apparatus, such as an increase in the ramifications of the cement glands, an increase or a decrease in the length of the oviducts. Likewise there was sometimes a slight effect on the secondary sexual characters, in that the ground color of the wings was somewhat darker than normal. When the anlage of any part of the accessory sexual apparatus was removed, that part was not present in the adult.

The transplantation of a testis into the body of a female from which one ovary had been removed was successful in only one case. The operation was done in the third caterpillar stage when the testis is still quite small and at a low stage of development. The testis developed normally in the body of the female and was found to contain mature sperm. The ovary was also well developed. The transplanted testis had no influence whatever on the external somatic characters, which were of the usual female type.

When one or both ovaries were transplanted into a castrated male, the development of the ovary was usually normal. Sometimes one or two of the ovary tubes failed to develop, owing probably to lack of room, since the ovaries were always best developed in the largest males, where there was most space. In 20 out of 111 moths with transplanted ovaries, the ovaries united with the vasa deferentia, one ovary with one vas deferens, or two ovaries united with one vas deferens or, in two cases, each ovary with a vas deferens. The histological structure of both ovary and vas deferens was normal, but the eggs never passed down the vas deferens. In one case, one testis was left at the end of a vas deferens and an ovary inserted in the vas deferens just below. They both developed normally, but the duct served as an exit for the sperm only, not for the eggs. The transplanted ovary had in no case an influence on the secondary sexual characters; the only difference between these moths and normal males was the fact that the eggs made the abdomen bulge somewhat.

Some experiments in transplanting were tried on *Orgyia gonostigma* because of its marked sexual dimorphism and because it remains in the caterpillar stage for about eleven months. Only two males survived the operation, and although the ovaries had been in the male body from September 11 till June 20 and were well developed, there was no evidence of any effect on somatic characters which were of the typical male sort.

Investigations as to the effect of the operation on such psychical characters as sexual instincts led to the conclusion that these characters are independent of sex cells and of parts of the sexual apparatus. In castrated moths, in moths deprived of their copulation apparatus, and in males with transplanted ovaries, the sexual instinct was found to be as strong as in normal males.

In another series of experiments, the anlage of the wing, a secondary sexual character, was removed at the time of castration in order to determine whether the new anlage laid down in the absence of sex cells would have the same sexual character as the old anlage laid down in the presence of the sex cells. In the control series, in which the sex cells were left intact and the anlage of the two wings of one side was removed after the second, third and fourth moults it was found that in one fourth of the cases there was no regeneration; in the rest, all amounts of regeneration occurred up to an almost complete wing, all of the regenerated wings being perfectly normal in markings which occurred in the same relative position as in the normal wing. From the fact that the whole wing is present in miniature and not merely the root of the wing is present, Meisenheimer concludes that the wing has not grown out from the stump of the old anlage which was left, but that a new anlage center has been laid down, perhaps by the old stump which has gained new relations with the tracheae. The difference in the amount of regeneration he attributes not to the amount of tissue left in operation, but to the length of time elapsing before pupation. In cases where this was shortest, about the time for normal moths, no regeneration took place; when this was somewhat longer (from 10 to 14 days longer) some regeneration took place; when this was longest (from 17 to 37 days longer) almost complete regeneration took place. The pupa period remained about the same as normal, whence the conclusion is reached that regeneration takes place during the caterpillar stage and differentiation during the pupa stage. In the castrated series, in which the wing anlage was removed, it was found that the wing developed its normal sex character, although no sex cells were present. There was a difference in the amount of regeneration just as in the control series. Likewise in males with transplanted ovaries, the regenerated wing was of the normal male type, and exactly corresponded with its unregenerated mate.

From these experiments Meisenheimer concludes that in these moths primary sex cells have no influence on secondary sex characters or on sexual instinct. He therefore does not agree with the theory that internal secretions from the sex glands affect the soma. Both primary and secondary sexual characters are to be traced back to the young germ cells, since the secondary are not influenced by the primary during ontogeny.

E. N. Browne.

ANTS

The last number in the Columbia Biological Series is a volume by W. M. Wheeler[1] on ants. It is the largest number in the series, containing nearly 700 pages, but the unusual interest of the subject justifies the size of the publication. After an introductory account of ants as dominant insects, the author devotes several chapters to their structure and development. Then follows a discussion of polymorphism in which the interesting problem of the non-reproductive worker in relation to heredity is fully elucidated. After this come chapters on the classification and distribution of ants and on their geological history. The remainder of the body of the text contains a most fascinating account of the habits of ants. Following a consideration of the habits of ants in general, of nest-building and of the ponerine ants, the most primitive and generalized type of modern ants, is a succession of chapters on special habits and relations. These include accounts of the driver ants, the Huns and Tartars of the insect world; the harvesting ants, which, though they are grain-gatherers, are not strictly speaking grain-planters; the fungus-growing ants, whose subterranean fungus-gardens are fully described and beautifully illustrated; the honey ants, some of which serve their colonies as living receptacles for stored sweets; and, finally, the slave-making ants, which in extreme cases come to be absolutely dependent upon their captive workers.

---

[1] Wheeler, W. M., "Ants, their Structure, Development and Behavior," New York, The Columbia University Press, 1910. pp. xxv + 663; 286 figs.

In appropriate places between the various chapters on these special groups are interpolated chapters on the supposed mutualism of ants and vascular plants, on myrmecophiles, of which among arthropods alone 1,500 species are known, on parasites, and on compound nests. The portion of the text dealing with the habits of ants is concluded by three remarkable chapters on the sensations, and instinctive and plastic behavior of ants, which, as a body of mature judgments on this most subtile field of animal investigation, is of the highest order. Any one who wishes to reach sane conclusions in the study of the habits of ants should ponder these chapters with care. The volume contains five excellent appendices: the first, on methods of collecting and studying ants; the second, a key to the subfamilies, genera and subgenera of North American Formicidæ; the third, a list of the described ants of North America; the fourth, on the extermination of noxious ants; and finally, a bibliography of over 2,000 titles. An ample index brings the volume to a close.

The brief outline of the subject matter of the volume as already given indicates the breadth of treatment accorded the material by the author. As a result the volume ought to find numerous readers beyond the professionals. Its pages throw many side-lights on human affairs which show that the sluggard is not the only one that might profit from the ant. Although the volume is based upon the studies of a world-wide range of myrmecologists, the reader is met at every turn with the author's extensive and intimate first-hand acquaintance with his subject. This acquaintance gives his critical comments unusual value.

In a book of such high general excellence it might seem ungracious to point out minor defects. As a matter of fact, however, the few that were noticed served only to increase the initial impression of thoroughness and accuracy. The illustrations, which are of the same high order as the text, are occasionally without any indication as to magnification (original Figs. 35, 37, 38, 39, etc.), and in a few other instances omissions occur, as in Fig. 271, in which the descriptive lettering of the legend is not repeated in the figure. In the text on page 108 *giantism* is probably a slip for the more usual *gigantism*. But even such slight defects as these are rare and the book presents an unusually clean appearance for a first edition. The treatment of the subject is so masterly and the material make-up of the volume so excellent that the biologists of this country may well look with pride upon this work as an American product.

G. H. Parker.

BOOKS **WILLIAM J. GERHARD,**

2209 CALLOWHILL STREET, PHILADELPHIA, PA.,

offers the following at affixed net prices. Extended catalogues of books and pamphlets in all branches of natural history post-free on request :

1.	American Journal of Conchology. 7 vols., partly bound	$25.00
2.	American Journal of Science. Second Series, volumes 1–10. Half roan (3 vols. somewhat waterstained)	10.00
3.	American Mineralogical Journal (Bruce). 1 vol., 1814. New half morocco	10.00
4.	American Monthly Microscopical Journal, vols. 1–20 (1888–1899), of which 14 vols. are half roan	15.00
5.	American Naturalist, vols. 1–6 (1868–72)	9.00
6.	Annals N. Y. Academy of Science, vols. 4–14 (1887–1898). Cloth	22.50
7.	Annuaire du Musée Zoologique de l' Académie des Sciences, St. Petersbourg, vols. 1–7 (1896–1902), lacking one number of vol. 1	10.00
8.	Bulletin American Museum of Natural History, vols. 1–11 (1887–1901)	27.50
9.	De Kay. Zoology of New York—Birds. 4to. Cloth. 141 colored plates	10.00
10.	Gaudry, A. Animaux fossiles et géologie de l'Attique. 2 vols., folio, 1862–67. Half calf, 75 plates and map	35.00
11.	Harlan, R. Medical and physical researches, etc. 1835. Cloth	7.50
12.	Journal and Proceedings Royal Society of New South Wales, vols. 11 (1877) to 23 (1890), except vol. 14. Partly bound in cloth	13.00
13.	King, C. United States Geological Exploration of 40th Parallel. Complete set, 7 vols., quarto, cloth, and two folio atlases	22.50
14.	Microscope (The), vols. 4–11. 8 vols. in four. Half roan	7.50
15.	Morton, S. G. Synopsis of the organic remains of the cretaceous group of the United States. 1834. Half roan. Rare	15.00
16.	Pritchard, A. History of Infusoria, including Désmidiaceae and Diatomaceae. Fourth (last) edition. 1861. Half morocco	8.00
17.	Proceedings Lit. and Philos. Society of Liverpool, vols. 1–34 (except vols. 5, 10, 11, 12, 16, 17, 20, 21), partly bound	16.00
18.	Reports of Explorations and Surveys . . . for a railroad from Miss. River to Pacific Ocean. 13 vols. 4to. Bound	12.00
19.	Smithsonian Miscellaneous Collections, vols. 1–6 (1861–67). Scarce	13.50
20.	Sowerly and Lear. Tortoises, terrapins and turtles drawn from life. Small folio, 1872. Half morocco, 60 finely colored plates	11.00
21.	Transactions American Entomological Society, vols. 1–6. Bound. Scarce	35.00
22.	Transactions Geological Society of Pennsylvania. 1 vol. (1835.) All issued. New half morocco. Rare	15.00
23.	Winter, G. Die Pilze Deutschlands, etc., vols. 1 and 2 (1884–87). Half morocco	7.50

Methods in Plant Histology

By CHARLES J. CHAMBERLAIN,

Second edition, revised and much enlarged; 272 pages, with 88 illustrations, 8vo, cloth; net $2.25, postpaid $2.39

THE first complete manual to be published on the subject of botanical microtechnique. It contains detailed directions for collecting and preparing plant material for microscopic investigation, setting forth the advantages and disadvantages of the different methods.

Will no doubt find a place in every well-regulated library, and will be found very useful by private students.—*Plant World.*

It is an excellent book for the individual worker and for classes in colleges.—*Education.*

A Laboratory Guide in Bacteriology

By PAUL G. HEINEMANN,

158 pages, interleaved, with 37 illustrations, 12mo, cloth; net $1.50, postpaid $1.61

A CLEAR and concise presentation of bacteriological technique, designed principally as a manual for the medical student, but highly useful also as a reference book for the biological teacher and investigator, as well as for practical workers in the fields of medicine and hygiene.

The instruction given is clear and accurate, and the practical exercises are well selected.—*The Lancet* (London).

A book such as this must facilitate very greatly the practical class work, for which it is most excellently adapted. — *American Journal of Medical Sciences.*

The directions are clear and concise, and every stage is described so carefully that it is hard to see how the student can go astray. Physicians who are rusty in bacteriology cannot do better than buy this little book. The book is beautifully printed and bound.—*American Journal of Clinical Medicine.*

Animal Micrology:

Practical Exercises in Microscopical Methods

By MICHAEL F. GUYER,

250 pages, 8vo, cloth; net $1.75, postpaid $1.88

THE title of this book will explain its scope. It is intended as a laboratory manual for textbook use. Its aim is to introduce the student to the technique of microscopic anatomy and embryology, emphasizing details of procedure rather than descriptions of reagents or apparatus. Sufficient account of the theoretical side of microscopy is given to enable the student to get satisfactory results from his microscope.

The directions are simple, explicit, and complete.—*American Journal of Clinical Medicine.*

The medical student will find it very useful as a guide to microscopic work.—*Journal of the American Medical Association.*

This is one of the cleanest works on microscopical technique we have ever seen, and is especially suitable for the beginner. It is full of points, tricks of technique not mentioned in other works, and is one that every student and physician should have.—*Medical Century.*

This valuable book is strong through its rigid exclusion of the trite and the conflicting. It is lucid and helpful, because a man long practiced in practical work has given what he believes the most expeditious and reliable method of obtaining a definite and comprehensive result. — *Medical Notes and Queries.*

A concise, eminently practical, and well-classified treatment.—*Science.*

The expositions of the methods recommended are admirably clear.—*Nature.*

One of the best and most practical works upon microscopic technique with which we are acquainted.—*American Naturalist.*

As a textbook it can hardly be improved. The research worker will find in this book just the information he frequently needs in preparing material with which he is not familiar.—*School Review.*

It does present in very clear form a judicious selection of methods, including an excellent untechnical account of the microscope and its optical principles, adequate for the undergraduate course in histology.— *Journal of Comparative Neurology and Psychology.*

ADDRESS DEPT. 64

Chicago THE UNIVERSITY OF CHICAGO PRESS New York

VOL. XLIV, NO. 522 JUNE, 1910

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. **The Botanical Society of America:**
  The Nature of Physiological Response. The Late Professor CHARLES R. BARNES - 321
  The Place of Plant Responses in the Categories of Sensitive Reactions. Professor FREDERICK C. NEWCOMBE - 333

II. **The Larva and Spat of the Canadian Oyster.** DR. J. SAFFORD . 343

III. **The Alimentary Canal of a Carboniferous Salamander.** Dr. ROY L. MOODIE 367

IV. **Shorter Articles and Discussion:**
  Observations on the Spawning Habits of Hydroides Dianthus. Professor CHARLES W. HARGITT - 376

V. **Notes and Literature:**
  Protozoa—Doflein's Lehrbuch der Protozoenkunde: Professor CHARLES A. KOFOID. Celebrating Darwin's Greatness and Darwinism's Weakness, V. L. K. - 379

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

TO ORNITHOLOGISTS

AND MUSEUMS

W. F. H. ROSENBERG

Importer of Exotic Zoological Specimens

57 Haverstock Hill, N.W., England

Begs to announce the publication of a new Price List (No. 11) of **Bird Skins.** This catalogue contains over 5,000 species, and is the largest and most complete price list of birds ever published. It is arranged in systematic order, based on the classification of the British Museum "Catalogue of Birds," with authors' names, indications of localities, and an index to families. It will be sent gratis and post free on application, as will the following lists:

No. 7, Mammals; No. 8, Birds' Eggs;
No. 9, Reptiles, Amphibia, and Fishes.

Largest stock in the world of specimens in all branches of Zoology.

Specimens sent on approval.

Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

Henry Holt & Company

34 West 33d St., New York
378 Wabash Ave., Chicago

Microscopes and Accessories

Hand Cameras of Highest Quality

Binoculars, Prism and Galilean

the best obtainable for Nature Study

Scientific Instruments

Laboratory Apparatus

Max Meyer 18 West 27th St. New York

"Quality, Prices, Service Right."

THE
AMERICAN NATURALIST

VOL. XLIV *June, 1910* No. 522

THE BOTANICAL SOCIETY OF AMERICA[1]

I. THE NATURE OF PHYSIOLOGICAL RESPONSE

BY THE LATE PROFESSOR CHARLES R. BARNES
UNIVERSITY OF CHICAGO

LIVING plants could hardly have been observed at all without recognition of the fact that they are affected by external conditions. These effects, when first observed, were undoubtedly interpreted as mere conditions of living, and our interpretation to-day has hardly gone beyond this. A moderate temperature, an adequate supply of water, and the normal light are necessary for green plants; and when these conditions are suitable the general behavior of the plant is affected. All its processes have a healthy *tone;* it flourishes; and the factors which operate to produce this condition are declared to be *tonic.*

When the effects of external agents are studied more closely, several peculiarities appear. Even these tonic factors are seen frequently to produce quite limited changes in behavior, though they may act simultaneously upon all parts of the body. Especially is this the case when there is some sudden change in the intensity or direction of these factors. Thus if the air temperature falls a few degrees on some spring day when the crocuses are in bloom, the perianth segments promptly curve inwards and close the flower. Or if the sunlight is obscured by clouds, the dandelion heads are soon folded together by the straightening up of the involucral bracts. No other changes are visible, though others may be detected by appropriate means.

---

[1] Invitation papers read at the sixteenth annual meeting of the Botanical Society of America, Boston, 1909.

Again, external agents may act on only a limited region of the plant, in which case the obvious effects may be restricted to some special part, either that immediately acted upon or one at a greater or less distance from it. Thus if the cotyledon alone of a *Panicum* seedling be lighted from one side, the hypocotyl, 20 mm. or more away, instead of continuing its equal growth, may curve abruptly.

In these two cases of limited visible change, the phenomena are explained by asserting that the protoplasm is *irritable* and *responds* to an external change called a *stimulus*. In fact, there is an inclination, after endowing the protoplasm with such "properties" as "irritability," "automaticity" and "self-regulation," to be satisfied with the words and there make an end. Such a tendency, wide-spread in the prescientific days, undoubtedly springs from the wonder with which one confronts an uncomprehended intricate mechanism. It finds expression, for example, in a common saying about this or that industrial machine: "It seems to have almost human intelligence." Of course no one supposes the machine really endowed with other than physical qualities, operating through the matter and the energy with which it is supplied. Yet the vitalism, which dominated the earlier years of physiology, even yet controls our speech and our thinking, and indeed lately shows signs of revival.

Vitalism, assuming living matter to be endowed with special powers, called vital in distinction from physical, is itself in part an expression of helplessness in the face of an uncomprehended mechanism, the living body, and in part an interpretation of nature in terms of our own consciousness. To seek explanation in that direction is to proceed from the simple to the complex; but the explanation of phenomena must be a process of analysis, not of synthesis, and so of necessity proceeds in the other direction. We may not believe it possible to account for the behavior of living things by considering them as mechanisms whose actions are to be described in terms of matter and energy; and certainly it is not possible to do this now for any but the simplest actions. Yet it must not be forgotten that all the progress that has been made has been made in this direction; so that it commends itself to us both by the *a priori* and the inductive method.

The phenomena of response are probably the most complicated to be seen in the plant, and as yet we are far from being able to describe them completely in terms of physics and chemistry. I purpose only to present some suggestions on the nature of these phenomena, as a contribution toward the mechanistic conception of the plant, in the hope that this presentation may help to rid us of some of the subconscious vitalistic notions that are apt to cling so persistently about our thought and speech.

First let us consider the relation of the phenomena of response in living and non-living matter. To speak of response by non-living matter can occasion no surprise. Sachs, long ago, in his "Lectures on the Physiology of Plants," pointed out the fact that response is not peculiar to living things, citing as an example the crystals of the yellow iodide of mercury, which change their constitution and color when stimulated by various agents—a scratch sufficing to initiate a change which spreads gradually through the whole. Many other substances behave similarly. To explain such a change we predicate a state of metastable molecular equilibrium, the upsetting of which at one point incites a spreading disturbance, as a row of properly spaced blocks fall.

There is another sort of response in non-living matter, which is conditioned by external factors. In moist air many anhydrous salts and oxids unite with water, and in some cases in proportions differing with the amount of the vapor pressure. Thus, anhydrous copper sulfate, at a temperature of 50° C. with the vapor pressure gradually increasing from zero, would take up one molecule of water and become the monohydrate as soon as the vapor pressure reached 4.5 mm. of mercury. As soon as it reaches 30 mm. the monohydrate takes up two more molecules and becomes the trihydrate; while at 47 mm. and above the trihydrate adds two more molecules and becomes the pentahydrate. Conversely, should the vapor pressure fall below 47 mm., the pentahydrate loses water and is transformed into the trihydrate, and so on. The constitution of the copper sulfate, in fact, precisely responds to the vapor pressure of water around it. Many like cases might be cited. The peculiarity of these is that while the external factor may change steadily, the physical response will be discontinuous. Among the multifarious phenomena of irritability in plants are some which are so nearly parallel to the behavior just described as to suggest an analogous causation.

It is possible that the application of the term irritability to the behavior of crystals will seem an unwise straining of its usual sense. Irritability has often been enumerated among the distinguishing properties of protoplasm. Even Sachs wrote:

> Irritability is the great distinguishing characteristic of living organisms; the dead organism is dead simply because it has lost its irritability.

But if we are to consider irritability as a property—a characteristic—of protoplasm, it must be understood to be a conditional property, as strictly limited by circumstances as are the properties of non-living matter. Steel may be highly tenacious at certain temperatures; but at the temperature of liquid air it is as brittle as glass and can be pulverized by a blow. A frond of *Laminaria* when wet is a tough flexible strap, but when dry it is so rigid and brittle that it can be broken to fragments by slight bending. Many a plant is clearly irritable at moderate temperatures when well watered and lighted, but loses its irritability completely under adverse conditions. Becquerel has dried seeds for six months in a vacuum with barium hydroxid at 40°, sealed them for a year in a glass tube exhausted to 0.002 mm. of mercury, kept them in liquid air at a temperature of — 190° for three weeks and in liquid hydrogen (— 250°) for three days. Is it possible to conceive of irritability existing under such conditions? Is it, indeed, possible to conceive of life as latent? I think not. Irritability must be counted as completely lost during this time, and as regained when the seeds germinated, as they did when suitable conditions were furnished. To emphasize the conditional nature of this quality, it may be better to describe protoplasm when irritable as in a state or condition, instead of following the example of the physicist in saying that it possesses the property of irritability, of which it may be as surely dispossessed as steel may be of its tenacity.

Of recent years Bose has the merit of having insisted upon the essential similarity of response in living and in non-living matter. His "Plant Response" and "Comparative Electro-physiology" are based upon this conception; and though they contain much that can not be approved, I am in complete accord with the thesis that plants are intelligible only as mechanisms whose behavior, though more complicated than that of non-living systems, is to be described by analogous laws.

While recognizing the essential unity manifest in the behavior of all matter, we must nevertheless discriminate between physical and physiological response. It is not possible, however, to use these terms as they have been used, even by Bose, to designate, respectively, the response of non-living and living matter, since many of the responses of organisms are purely physical. Physical response, as I conceive it, is marked by the fact that the energy applied to the body is a full measure of the effect produced. Thus, when the conductivity of a selenium plate is altered by light, the molecular disturbance (if we so explain it) is initiated by the radiant energy, and the effect is precisely measured by the energy applied from the outside. The selenium contributes nothing. It is acted upon, and its condition is altered for the time being, by the external agent. The effect dies out shortly after the agent ceases to act. Whether there is a loss of energy or a gain, no further change ensues in the system, unless it is acted upon from the outside.

Physiological response, on the other hand, though at bottom of the same sort, differs in that the external agent produces an upset that releases energy previously accumulated, so that the effect exceeds that due to the initial energy acting upon the organism. That is why, indeed, the term *stimulus* was originally applied to such an agent; it brings into action energy often vastly greater than its own. In this case there is a run-down of energy. The system contains less than before by as much work as has been done in response to the stimulus. Repeated responses lead to exhaustion of the accumulated energy, when further stimulation is impotent. To explain such a situation Bose's theory of molecular strain is inadequate; we are driven to take account of stored energy, and not a direct supply. For if the depleted system be kept under conditions as nearly uniform as possible, it proceeds to recover energy by the incorporation of new material with its potential energy. The protoplast assimilates food and presently is ready for new response to any stimulus. It is the cyclic character of their energetics that characterizes living things, no less in the phenomena of response than in nutrition.

Even a casual examination of the various responses of an organism shows clearly that some of them are to be classed with the physical and others with the physiological, as above defined. If so, it is plain that it is not mere responsiveness that marks living things, for non-living matter responds; it is the ability after a loss of energy by response to regain, by the aid of the environment, a condition which makes response possible once more. This is no mere restoration of a molecular equilibrium which has been disturbed or relief from molecular strain; it involves acquisition of energy. How far this is due to a direct intake of energy and how far to the utilization of potential energy in available foods, our present knowledge of the energetics of plants does not enable us to decide. Certainly we can not accept the source proposed by Bose, when he writes:

> And now we see that the fine ramifications of fibrovascular elements over as wide an area as possible in the leaf provides a virtual catchment basin for the reception of stimulus. The expanded lamina is thus not merely a specialized structure for the purpose of photosynthesis, but also a sensitive area for the absorption of stimulus, the effect of which is gathered into larger and larger nerve trunks in the course of its transmission downwards into the body of the plant.

It is of course possible to use the term *stimulus* to designate any external or internal agent that produces an effect upon the organism, and *response* for the effect produced; but that use of the terms tends to confusion. Yet, besides the erratic treatises of Bose, some recent text-books use the words in this way. One, for example, reads: "Responses to water stimuli.—The primary responses of the plant to the water of the habitat are four: namely, absorption, diffusion, transport, and transpiration." It is hardly necessary to point out that if such processes are responses, then every change that occurs in nature is a response and every agent a stimulus. By such a usage we should lose the whole value of the discrimination embodied in the terms.

The less clearly plant processes are conditioned by the environment, the more likely they are to be reckoned responses to stimuli. Growth, for example, is often considered a response to stimuli; but it seems most likely that it is quantitatively determined by various factors (turgor, temperature, oxygen, food, etc.), any one of which may limit it. Stimulation by gravity or light may be an added factor, interlocking with one or more of them, and, by inducing local variation in the rate of growth, producing curvature; which is obviously a physiological response, for when the effect of the stimulus passes away the ordinary rate may be resumed.

In considering the energetics of response, it is essential not to forget that many stimuli *inhibit* actions going on at the time excitation occurs. There are many familiar examples of this among animals, but few in plants.

One well known is the interference of stimuli in tendrils. As Fitting showed, friction on the dorsal side of tendrils which usually curve after irritation of the ventral side, inhibits the curvature, not by setting up a countervailing rate of growth, for it apparently has no power to influence growth, but by interfering with the reaction somewhere between perception and the growth response. Here, if the stimulus were a source of energy, or limited the reaction, the double excitation should produce a doubly strong response. Nor can the well-known interference of light or sound waves in unlike phases be cited as an analogy of the inhibition in this case, because no such superposition is possible. It must be admitted that in cases of this kind the energy of the stimulus is not directly related to the response.

Of course, in urging this I must not be understood as denying that the excitation is often proportional to the intensity and duration of the stimulus, and that the final response may be influenced by the amount of excitation; the point is only that potential energy is released in amounts not at present referable quantitatively to that of the stimulus.

On analyzing the varied reactions to stimuli, it will be found in many cases that it is possible to recognize two well-marked phases, which may be designated *primary* and *secondary*. In other cases no such distinction can be made. One of the primary phases of response is known as *perception*, a word which, as used by plant physiologists, is entirely without psychological implications. Whatever change in the protoplasm is connoted by that term takes place almost instantly, as shown by the phenomena of summation. Stimuli of extremely brief duration—say a small fraction of a second—so transient that they produce no observable effect, nevertheless, if repeated at proper intervals, finally give rise to a reaction. The brevity of each period of stimulation gives indication of the speed of the perception change; for if no effect were produced by a single stimulus, repetition could have no effect.

Another primary phase of response is the propagation of the excitation. The disturbance called perception propagates itself, that is, it initiates in adjacent material a corresponding change, progressing from point to point, as shown by secondary effects produced at a greater or less distance from the point where the stimulus is applied. The precise character of the change itself has been little studied in plants, though the rate of propagation is known to be of the same order of magnitude as that in the nerves of the lower animals—say 1 to 10 mm. per second.

The secondary phase of response is manifested either separately by turgor mechanisms and by growth mechanisms, or by the two conjointly. In turgor mechanisms altered turgor of the cells in a definite region causes displacement of parts attached. In growth mechanisms local differences in the rate of growth of the organ displaces the adjacent parts. When combined the earliest displacement is due to turgor, and this is made permanent by growth.

Examples are so familiar that they need hardly be cited, and a single one of each will suffice. When the tip of a leaflet of *Mimosa* is stimulated by burning with a lens, the excitation is propagated to the petiolule of the leaflet, the turgor of its upper and anterior cells is so reduced that those on the opposite side compress them, bending the petiolule sharply and so carrying the leaflet forward and upward. The disturbance may spread to other leaflets and even to the base of the petiole, with appropriate curvatures in each motor organ.

When a primary root is placed horizontal, perception occurs mainly in the tip, the excitation is propagated backward, and the secondary response appears as differential growth of the cells chiefly in the third and fourth millimeter from the tip, which produces the well-known curvature.

Though much discussed, it is not clear whether the secondary response of tendrils depends on a growth mechanism or a turgor mechanism. I am inclined to believe that there is here a combination, the first curvature being due to a turgor change, which is fixed with unusual promptness by growth.

The movements of minute motile organisms, whether autonomous or induced, can hardly be analyzed, so intimate are the relations of the primary and secondary phases of response, if indeed they are separable.

All physiological responses when analyzed show the same general relations, no matter how varied the stimuli and the end reactions. If there were nothing more than the general applicability of Weber's law, this would be enough to suggest that there is some fundamental unity in the responses. There are, however, many other features that point in the same direction. It is obvious that the common factor is not to be found in the later phases of the response, where the structure of the organ may play a determinative rôle; nor in the direction from which the stimulus acts, which is known to determine often the direction of movement. Bose has sought to show that all cells when stimulated exhibit two concomitant responses, by which, it seems, he would account for all the phenomena of plant life, even to the ascent of water! Without assenting to his applications of the observations, we must say that Bose has done good service in showing that a mechanical contraction follows stimulation, and that change in electric potential occurs simultaneously. This, I think, we may consider established for a large number of plants, and it is very likely true of all. A study of the negative electric variation leaves us quite in the dark as to its significance, and though we are constantly tempted by electric analogies in the description of nervous phenomena, we gain no real insight yet into the rôle of electric stresses in organisms, because our knowledge of their causation is too vague.

In concomitant contraction and electric variation we have a two-phase phenomenon, which should be capable of further analysis. Is there any simpler action—more fundamental—which may produce both? To this question the recent work of Lepeschkin and Tröndle, supplementing earlier investigations, suggests an answer. Turgor variations have long been studied, but a reason for them has been sought in vain. We now know that various agents change the permeability of the protoplast to solutes, and that this sensitiveness is not limited to the specialized cells of a gland or a motor organ, but characterizes even the mesophyll. That this behavior occurs where there is no obvious relation to the functions of the organ, suggests at once that it inheres in the protoplast as a fundamental quality, in virtue of its chemical constitution or its molecular structure. It is perfectly easy to understand that this structure may be modified by the radiant energy already known to alter the permeability of the protoplast; and many other stimuli are of a kind to influence the unstable chemical compounds that compose protoplasm. If that estimate be verified by further researches, we shall be justified in considering *variability in permeability* as a basic property of protoplasts.

It will be evident enough that a change in permeability will permit the escape of some of the cell sap, with consequent shrinkage of the protoplast, stretched as it is by osmotic pressure, so that Bose's contraction would naturally result. Whether the escape of the solutes would account for the negative electric variation, I do not pretend to say, for the present theories as to electromotive force do not afford any light on the situation. Therefore, until the relation of electric stresses to other phenomena is better known, we must leave this question in abeyance.

The primary and secondary phases of a response may be understood readily in conformity to this conception. The sufficient stimulus or the summated excitation changes the constitution of the protoplast, and this change spreads along the protoplasmic lines of communication, until it reaches a region where the changed turgor results in a curvature, either directly, as in turgor mechanisms, or indirectly, by altering the rate of growth, as in growth mechanisms. That the turgor changes reported in the root undergoing geotropic curvature apparently do not harmonize with this theory is probably due to the untimeliness of the observations. It is said that when the curvature is taking place the turgor of the cells on the concave side is unchanged and on the convex side lowered. But by the time curvature is well under way, the turgor conditions immediately following excitation may have undergone complete alteration, if we may judge from similar changes in motor organs. Thus, the original turgor, lowered on excitation (according to theory) by the increased permeability of the under side, may have been regained, while the very growth itself of the convex side may be responsible for the reduced turgor then observed on that side.

The responses of recoil and orientation in motile organisms are easily interpretable in terms of this conception, and though the application is purely hypothetical, it is no more so than the current explanations. Just such a change as results in changed permeability of the walled protoplast to solutes of the great vacuoles might take place on the passage of a naked protoplast into or out of a stimulation zone. How such a change can reverse the mechanism of movement is not explicable at present; but the new conception introduces no new difficulty. For example: If a change in surface tension is predicated as the result of excitation and the occasion of recoil, it is just through some change in chemical constitution that such an alteration in surface tension might come about. If the organism be one which orients itself to one-sided stimuli, orientation may as easily result from a local change in constitution as in any of the ways assumed by current theory.

No one is more keenly aware than I that these all are matters of speculation. They are presented as such. My hope is that they will direct attention to this phase of plant behavior and will stimulate thought, which should first clarify our conceptions, and then suggest lines of research.

II. THE PLACE OF PLANT RESPONSES IN THE CATEGORIES OF SENSITIVE REACTIONS

PROFESSOR FREDERICK C. NEWCOMBE
University of Michigan

More than two decades ago in the hands of Darwin, Sachs, Wiesner, Pfeffer, Strasburger, Stahl and others, the principal sensitive reactions for both fixed and free-moving plants had been determined. At that period, in animal biology only a few scattered papers had appeared on sensitive reactions. The zoologists approached this study through human psychology; starting with intelligence and reflexes in the highest animals, they cast a glance now and then toward the lower metazoa, and talked of reflexes and instinct. Plants, not standing in the line of descent which has its climax in man, were studied in an objective manner with no attempt to bring their reactions into a scheme of comparative psychology.

For the past two decades more attention has been paid to the study of behavior in the lowest animals, with the result that a great body of literature has already arisen, some of it tainted with anthropomorphism, but the most of it describing simply and carefully the reactions of the protozoa and the lower metazoa.

This independent activity on the part of the plant and animal biologists has resulted in the upbuilding of two almost independent bodies of literature on the behavior of lower organisms. Such early workers in the field as Verworn and Loeb compared and identified the reactions which they saw in the lower animals with those already published for plants; but as the zoologists have worked on, and more workers have come into the field, there has arisen among the botanists a feeling of uncertainty as to the significance of the terminology employed by the zoologists, and a hesitation in identifying plant reactions with those of the lowest animals. Thus, Francis

Darwin, in his presidential address before the British Association for the Advancement of Science in 1908,[1] intimates that he does not understand Loeb's use of the term "tropism." Botanists, probably quite generally, are in doubt as to whether Jennings's "trial and error" description can be applied to plant reactions. The existence of these two bodies of literature, and the uncertainty as to the significance of terms, calls, to my mind, for an examination of the phenomena of response in plants and in the lower animals, to the end that doubt may be removed as to the applicability of the same terms to both plant and animal response.

Proceeding to compare these two groups of organisms, we may say that both have fixed and free-moving forms. Most of the plants are fixed, and a group of their well-known reactions which botanists call "tropisms" are exactly simulated on the animal side by hydroids, as recorded by Loeb.[2] Geotropic and heliotropic bendings of the so-called stems and the so-called roots of the hydroids differ in no way from the manifestations of these phenomena in the stems and roots of plants.

Most of the lower animals are free-moving, and it is upon the phenomena of movement in these forms that the most of the animal studies have been made. Among plants, corresponding studies have been made upon the movements of bacteria, antherozoids and the swarm-cells of algæ and fungi. A study of the literature describing the behavior of the protozoa and of the free-moving plants must convince one that the stimuli and the responses are the same in both divisions of organisms. There are animals with amœboid movements and plants with amœboid movements, both animals and plants with cilia, and both with flagella. We may go a step farther, and consider the stimuli that influence the movements of these plants and animals. We have learned that both are directed in their behavior by gravitation, light, chemicals and the electric current. The behavior in the plant group can be described by the same terms as used for the animal group.

---

[1] *Science*, XXVIII, 353.

[2] "General Physiology," I, 103.

Before proceeding farther in the comparison of plant and animal responses, we must consider the relation of responses in fixed forms to those in free-moving forms. It is well known that botanists generally use the terms "tropism" and "taxis" to distinguish movement in the fixed organisms from that in the free-moving. Some zoologists also, among them Verworn, observe the same practise. The majority of zoologists, however, following the lead of Loeb, omit the "taxis" designation wholly, and include the movements of both fixed and free-moving forms in the term "tropism." This is merely a question of terminology, and need not occupy our time here. It is more important to consider whether the behavior of the fixed and that of the free-moving lower organisms are enough alike to be regarded as fundamentally the same. We may cite an analogy by saying that a traction engine may one hour be pulling a load along a road, and the next hour it may be stationary and operating a threshing machine. To enable it to do the one or the other requires but a slight alteration in the form of connection of its parts, a slight change in its mechanism. A swarm cell of the alga, *Ulothrix,* may alter its direction under the application of a slight stimulus, and swim toward the source of light. It may, a short time later, fix itself to the substratum, and now bend as a fixed organism toward the source of light. One can readily believe that the two reactions are the same except for the difference in the mechanism.

Besides the evidence for the fundamental similarity of sensitive processes in fixed and free-moving organisms furnished by the foregoing example, is the evidence presented by the quality of relation of stimulus and response in the two kinds of organisms: Both kinds of organisms, according to their structure, show simple positive or negative movements toward or away from the source of stimulation; both kinds are sensitive to the same kinds of stimuli, such as gravitation, light and chemicals; and both kinds vary their response according to their *physiological state.* In the various published observations which treat of the reactions of fixed and free-moving organisms, the authors regard the responses as belonging to the same class; and we may so regard them here. It might be said also, that the majority of reactions in the middle and higher metazoa are regarded by some as the same in kind, differing only in degree from the reactions of the protozoa. With the more complex reactions of the higher metazoa, botanists have little to do.

What now are the characteristics of these sensitive phenomena in plants and animals by which we class such phenomena together?

1. On both the plant and the protozoan side, the organisms possess no nerve cells. We used to be taught that for a reflex action there must be an afferent nerve, a ganglion and an efferent nerve. Such a chain is no longer necessary for a reflex according to definition. Pfeffer speaks of reflex acts in plants, and Massart, Jennings, Bohn and others expressly state that the tropisms of plants and nerveless animals are to be denominated reflexes, or, more specifically, *non-nervous reflexes.*

2. By the term "tropisms" (including "taxims"), the botanist has understood those direction movements of plants due to external stimuli, such as gravitation, light and chemicals. But this use of the term is now too broad.

The zoologists apply the same term to similar movements of the lower animals. But not all zoologists adopt the definition of a tropism as the definition is understood by the botanists. To the botanist, "tropism" always implies a response due to what is known as the *indirect* action of a stimulus; that is, the stimulus produces first an excitation, the excitation sets up a wave, or impulse, which is transmitted to the reaction protoplasm, whose action gives the sensitive response. The controversy over the implied meaning of "tropism" as applied to animals seems to have arisen mostly through the attempts of Loeb and his followers to simplify the conception of the sensitive processes, to conceive of the stimulus as *directly* producing the reaction, as one might think of a heliotropic curve in a marine annelid produced directly by the sun's rays shortening the muscles on the sunward side. The controversy among the zoologists wages about the terms *direct* and *indirect*. Indeed, the banners of the opposing forces may be said to bear respectively but these two mottoes. On the one side the herald has proclaimed these terms to the satisfaction of the botanists; that is, all sensitive reactions are *indirect;* that is, they are complex, the stimulus producing a change in the protoplasm, local or wide-spread, and this excitation of protoplasm producing an impulse, over a lesser or greater distance, setting in operation, or releasing, energy which brings the visible response. On the other side, the terms are but obscurely defined, and the nearest we come to a definition is that the excitation and the reaction are local.

Among plants there may be cases in which the excitation and reaction are local, and there are certainly cases in which a considerable part of the plant is affected. Rothert, experimenting with the coleoptile of the oat, found that he could induce positive heliotropism when only the basal, motile, part was illuminated, the rest being shaded; or he could obtain the same reaction when the basal part was shaded and only a millimeter of the tip of the leaf was illuminated. In the former case, for aught we know, the whole process was local; in the latter, it certainly was not local. Yet there is no doubt in our minds that the processes were the same in both cases. In both cases there were excitation, conduction, reaction; only in the latter case, the excitation was in a different part of the plant, and the conduction was over a greater stretch than in the former. Yet it is over the differences which these two illustrations show that the controversy has arisen over *direct* and *indirect* response. A case known to occur in plants seems to me to illustrate fairly well the so-called *direct* response of the zoologists: The leaves of some plants roll up when illuminated by the hot sun, due to the loss of water on the illuminated side. This is certainly *direct*, but most biologists would call it a mechanical, and not a sensitive response.

It has already been said that botanists accept the *indirect* method as applying in all cases to plants; and almost all zoologists take the same view with regard to animal reactions. We may conclude, therefore, that the term "tropism" may be used in the same sense for both plants and animals. The "tropism" resulting from direct action has not yet been demonstrated for either plants or animals. This conception of the significance of the term "tropism," as presented in the foregoing paragraphs, is not simple, but very complex; and in attempting to analyze the behavior of organisms, we meet with several conditioning phenomena, some of which may now be described. The terminology used in the following paragraphs is taken mostly from the zoologists, and botanists will note that the same terms are applicable to plant response.

One of the most widely extended of these observed phenomena is the variability of the response when the same external conditions are operating. Thus, Strasburger found the swarms-cells of *Ulothrix* and other algæ, during their early active period, positively heliotropic, but negatively heliotropic during their later active period. The change in *disposition* of the peduncle of the poppy, of the *Narcissus*, and of the members of various other plants, is familiar to all botanists. All of the foregoing changes in disposition can be referred, for want of a clearer understanding, to internal changes incident to age. These internal conditions which influence the response to external stimulus are called also the *physiological state*. The foregoing examples are illustrations of the influence of *physiological state* on response.

The physiological state may also be altered, and hence the reaction of the organism may be altered, by an external agent which is not the stimulus to response. The rhizomes of *Adoxa* and *Circæa,* in normal surroundings growing horizontally because of their diageotropism. become positively geotropic when exposed to light, and grow toward the earth. The rhizomes of some other plants, in similar treatment, become negatively geotropic. Experiments have shown that these changes of direction in growth in these rhizomes are not heliotropic, but due to a change in disposition toward gravitation. Light does not cause the bending, but changes the physiological state, and gravitation causes the bending. Another illustration of a change in disposition due to external agency is furnished by the behavior of seedling peas and vetches which become more heliotropic when the atmosphere contains small quantities of illuminating gas, or of carbon monoxid. Loeb found that *Volvox,* some crustacean copepods and other organisms, are rendered more responsive to light by putting a weak solution of carbon dioxide, acetic or hydrochloric acid, in the water in which they are swimming. This author suggests that this influence on the physiological state[3] is due to the acid preventing the formation in the organism of some anti-positive substance, normally generated. This hypothesis may not be supported by future study, but there is some evidence offered in its behalf, and it is a worthy attempt to come a step nearer to the intimate processes.

The "trial and error" hypothesis as applied by Jennings to some phenomena of behavior in protozoa is defined by him as "the selection through varied movements of conditions not interfering with the physiological processes of the organism."[4] The term itself, "trial and error," has lately been abandoned by Jennings,[5] but the value of the hypothesis as describing behavior he still maintains. It is plain to see that the so-called direction movements, or tropisms, as they have been generally recorded for our fixed plants, can not have their behavior included in this category; for by them there is apparently no *selection through varied movements.* Our typical plant tropisms show that one movement or curve, and that is unvaryingly toward the assumption of the new position of equilibrium. The response is what Bohn has called *resistless.* The term is expressive, and may be useful; but we must not forget that all reactions of lower organisms are resistless.

---

[3] *Archiv f. Physiol.,* 115, 1906, 564.

[4] "Behavior of the Lower Organisms," 1906.

[5] AMER. NATURALIST, October, 1909.

There are recorded, however, the results of two series of experiments with plants which seem to me to range themselves with the phenomena described as ''selection through varied movements.'' I refer to the establishment of half-hourly geotropic rhythm in the stems of *Taraxacum* and valerian, and of quarter-hourly heliotropic rhythm in the cotyledons of *Phalaris* and *Avena,* by the work of Francis Darwin and Miss Pertz. If there is doubt as to whether the rhythms just noted illustrate the first part of Jennings's hypothesis for the description of the origin of behavior, namely, ''the selection through varied movements of conditions not interfering with physiological processes,'' there can, I believe, be no doubt that the establishment of these rhythms illustrates the second part of the hypothesis, namely, that the ''resolution of one physiological state into another becomes more rapid after it has taken place a number of times.'' The gradual shortening of the period of oscillation, in the plants used by Darwin and Pertz, till the half-hourly or quarter-hourly rhythm was established, seems to me to express the more rapid resolution of one physiological state into another.

Though the idea of trial and error seems capable of application to but few of the recorded reactions of fixed plants, it is descriptive of the movements of bacteria, swarm-cells and spermatozoids. For these plants, by varied movements, finally arrive at a condition of the environment which does not interfere with their physiological processes.

Another descriptive for a group of phenomena in behavior, used in both botany and zoology, but in quite different senses, is *differential sensibility.* Pfeffer applies this term to all of the tropistic processes of plants, including the typical tropisms and the shock-movements; and it is, as he says, true that it is only by a perception of difference in the stimulus on the two sides of an organism that we obtain any tropism. On the other hand, Nagel uses the same term—Unterschiedungsempfindung—in application to the shock-movements alone. Jennings, I believe, uses the term in Pfeffer's sense, Loeb and Bohn with nearly the same meaning as Jennings's *trial* and *error* idea, or, at least, they would claim that the *trial* and *error* phenomena are a combination of tropisms and responses to *differential sensibility.*

To Summarize: In considering the foregoing phenomena, only the so-called *direction movements* of fixed organisms and the locomotory movements of free-swimming organisms have been referred to.

The organisms considered—plants and protozoa—have no nerve-cells, but nevertheless, their reactions are, and may be, spoken of as *non-nervous reflexes.*

While the responses in *fixed* and *free-moving* organisms are different in their external manifestations, the relations of stimulus and response and the conditions of operation of stimulus and response are much the same in both classes of organisms.

The terminology as introduced and generally used by botanists has been chosen as mere designation of the obvious stimulus and the direction of movement of the organism. Hence *tropism* or *taxism* is used to designate all the responses which animal biologists, with closer attention to details of behavior, have subdivided into a larger number. In botany, therefore, the term *tropism* should be used in a more restricted sense than at present.

In both plant and animal behavior, this term may be restricted to those simple movements which result in placing the organism in a certain direction with reference to the direction of the stimulus.

The term *fright-movement* or *shock-movement* or *recoil* (or a still better one) may be used to describe those responses due to a sudden change in the environment. Some of these shock-movements are doubtless tropisms, but perhaps not all. These are the movements that are due to differential sensibility (Unterschiedungsempfindung) in the sense of Loeb, and to transition stimulation (Uebergangsreizung) in the sense of Pfeffer.

There might also be some designation for the series of responses which Jennings attempted to name as "trial and error," a complex of tropisms and shock-movements, influenced by a varying physiological state.

Very recently Bohn has proposed to account for all behavior of lower organisms under four designations: *mechanical reflexes* (tropisms), vital rhythms (a group of *autonomous movements* of the botanists), *differential sensibility* and *associative phenomena.*

The ideas contained in these terms are all illustrated by plant behavior. But the terms are inadequate, for they are not coordinate. Some of them refer to responses, some to physiological state.

Before closing, reference might be made to Semon's book, "Die Mneme," the ideas in which, especially regarding *associative phenomena* in behavior, aid one in gaining a possibly clearer conception of the origin of some reactions of organisms.

Besides the reactions treated in the foregoing pages, for which a harmony has been attempted between the students of plant and animal behavior, we all know that there are groups which need a better and more expressive terminology than now is in use. As an illustration of phenomena needing more precise terminology, I might refer to the reactions known as epinasty and hyponasty. A very complete and apparently adequate terminology for all sensitive, non-nervous, reactions is given by Massart in *Annales de l'Institut Pasteur,* 1901, and a translation of the same in *Biologischem Centralblatt*, 22, 1902, 9.

THE LARVA AND SPAT OF THE CANADIAN OYSTER

J. STAFFORD, M.A., PH.D.
McGILL UNIVERSITY

II. THE SPAT

IN the first part of this article, dealing with the larva,[1] I have already indicated that, in the progress of my research, it soon became necessary to plan means of procuring young oyster spat for comparison with my supposed oyster larvæ before I could feel satisfied that the latter were in reality larvæ of the oyster. Of the common bivalve mollusks only Ostrea and Anomia live fixed to objects of support, so that the matter has some appearance of simplicity in the fact that all free-living forms may be eliminated. But careful examination of eel-grass, rock-weed and other marine plants, of shells, stones, timbers and other objects revealed no young spat, and I was forced to wonder where the oyster secreted itself at this stage of its life. I examined sand with the microscope to find if, like many bivalves, the young oyster might burrow for a time, but with no better result. Bundles of brush were tied to submerged rocks, or weighted with stones and sunk at various places. These were examined at intervals but without success. Each failure suggested some new possibility that required examination and occasioned delay. Time was flying, it was getting late in the season, and each day brought no further progress. What stupendous obstacles present themselves to the investigator and how simple after one has once mastered them!

A copy of Jackson's work,[2] procured for me at this time by Professor Wright, was particularly opportune, and I owe to it much by way of information and suggest-

---

[1] AMER. NAT., XLIII, Jan., 1909, pp. 31–47.

[2] See literature 12 of part I.

EXPLANATION OF PLATE

The plate accompanying "I. The Larva" was intended to be lithographed of the same size but was reproduced smaller and lost detail. I find from measurements the figures are magnified about 30 diameters. To agree with it the figures 1, 2, 3 of this plate, "II. The Spat," are magnified 30 diameters.

FIGS. 1, 2, 3. Young spat of Canadian oyster from the right (upper) side as they occur attached. Magnified 30 diameters.

FIG. 1. Oyster spat .5 mm. high, showing larval and spat shells.

FIG. 2. Spat 1 mm. high. The larval shell grows no larger, the spat shell grows to the adult size. Many organs are sketched in but the liver is left out, as it would obscure other parts.

FIG. 3. Spat 1.5 mm. for comparison.

FIGS. 4–12. Transverse sections of oyster spat 1 mm. high (compare Fig. 2), viewed from behind so that left and right of the figures correspond with the observer. The sections are in order from anterior to posterior but are not successive. The shells had been decalcified and are somewhat diagrammatic, thin left and thick right valve.

FIG. 4. Section through region of upper lip and transversely to anterior filaments of left inner hemibranch.

FIG. 5. Through mouth, unmarked parts same as preceding. The lower lip is borne by the anterior end of the abdomen (region of the foot).

FIG. 6. Mouth open at right, closed in to œsophagus at left. Rudiments of upper and lower palps.

FIG. 7. Œsophagus and tips of filaments of right inner hemibranch.

FIG. 8. Abdomen with five liver-follicles about the œsophagus.

FIG. 9. Through center of stomach showing œsophagus about to enter it, origin of intestine and right and left stalks of liver. Three other liver follicles are shown as well as the inferior lobe of the stomach, the visceral ganglia and the left inner hemibranch.

FIG. 10. Through anterior edge of adductor muscle, posterior end of gill.

FIG. 11. Through adductor and tip of inferior lobe of stomach. Several liver follicles.

FIG. 12. Posterior edge of adductor with rectum descending.

FIGS. 13-18. Transverse sections of spat 2, 2.5, 3, 3.5, 4, 5 mm. high. Not equally magnified. Left valve often damaged or left attached.

FIG. 13. Through mouth of 2 mm. spat, showing labial palps.

FIG. 14. Section of 2.5 mm. spat, touching anterior edge of adductor, showing the supra-branchial slit leading out from the supra-branchial cavity on the right side and the rudiment of the right outer hemibranch. Right and left inner filaments are cut longitudinally.

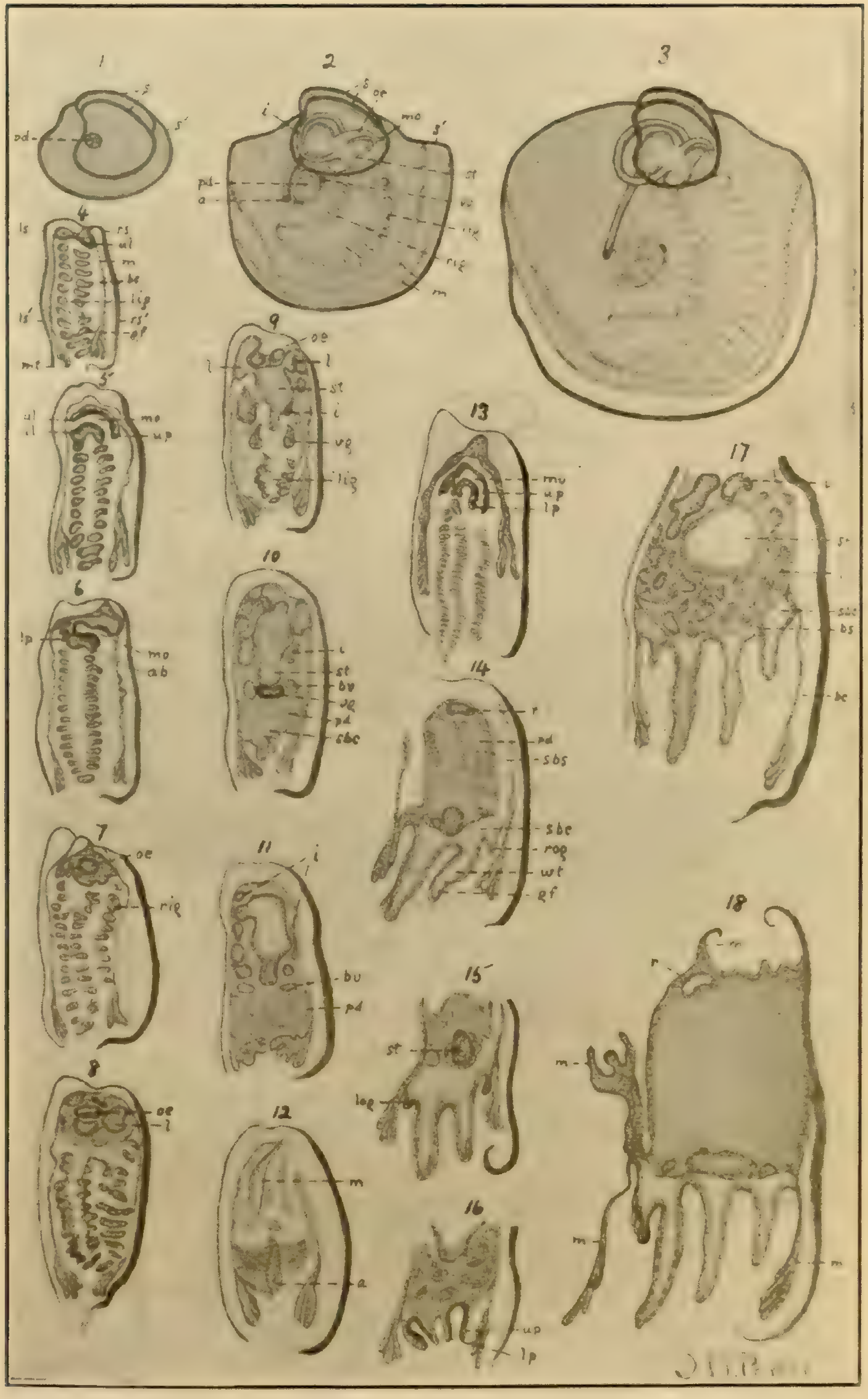
FIG. 15. Similar section of 3 mm. spat but slightly in advance and cut short above, showing rudiment of left outer hemibranch.

FIG. 16. Slightly behind mouth of 3.5 mm. spat, cut off above, to show all four labial palps. Liver follicles and portion of stomach above.

FIG. 17. Through 4 mm. spat, showing septa between supra-branchial cavities of inner and outer hemibranchs, the position of the original ctenidial axis.

FIG. 18. Section of 5 mm. spat through adductor muscle and visceral ganglia. The upper free edges of the mantle right and left of the rectum are very irregular. The branchial septa stop short of this section so that the supra-branchial cavity is continuous above all four hemibranchs.

a, anus; *ab.* abdomen; *bc*, branchial chamber; *bs*, branchial septum; *br.* blood vessel; *gf*, gill filament; *i*, intestine; *l*, liver, *lig*, left inner hemibranch (gill); *ll*, lower lip; *lp*, lower labial palp; *ls*, left valve of prodissoconch (larval shell); *ls′*, left valve of dissoconch (spat shell); *m*, mantle; *mo*, mouth; *mt*, mantle tentacle; *oe*, œsophagus; *pd*, posterior adductor muscle; *r*, rectum; *rig*, right inner hemibranch (gill); *rs*, right prodissoconch; *rs′*, right dissoconch; *s*, prodissoconch; *s′*, dissoconch; *sbc*, supra-branchial chamber; *sbs*, supra-branchial slit; *st*, stomach; *ul*, upper lip; *up*, upper labial palp; *vg*, visceral ganglia; *wt*, water tube.


1
s
s'
pd
2
s
oe
i
mo
s'
st
pd
a
v
lig
rig
m
3
4
ls
rs
ul
m
bc
lip
ls'
rs'
gf
mt
5
ul
ll
mo
up
6
lp
mo
ab
7
oe
rig
8
oe
l
9
oe
l
l
st
i
vg
lig
10
i
st
bv
vg
pd
sbc
11
i
l
bv
pd
12
m
a
13
mo
up
lp
14
r
pd
sbs
sbc
rog
wt
gf
15
st
log
16
up
lp
17
i
s
sbc
bs
bc
18
m
r
m
m
m

iveness. The method of putting out glass[3] for the reception of fixed forms of animal life I had already become acquainted with at St. Andrews while working on the clam, but the present was the occasion to try every means that could be devised and quickly applied. I accordingly took what objects could be easily procured and constructed and set out traps calculated to capture full-grown larval oysters at the time of their fixation. The idea is the same throughout all forms of the method; the particular turn in application was my own. Window-glass was cut into strips 2×6 inches so as not to be too big to use on the stage of a compound microscope, the advantage of glass being that one can use either transmitted or reflected light and can turn it over so as to see, through the glass, the attached side of the oyster. These strips were stood on end in deep crocks, about a dozen in each crock, and kept from falling against one another by wire racks, the object of placing them vertical being to minimize the aggregation of sediment on their surfaces. The traps were then planted at various places where there were oysters—off Curtain Island where the oysters were large, and off Ram Island Point where there were many sizes of young oysters. The crocks were sunk in gravel just below low-tide level and made secure against the buoyant force of water and the lateral action of waves and currents by building stones around them but leaving the tops open. It was thought that larvæ, either swimming about or swept about by the waves, might drop into the crocks where the water would be comparatively still and find it easy to cling to the glass during the first stages of fixation.

Ram Island Point appeared to be the most favorable place and that was about six miles from the station, but daily visits were made, the strips of glass were one by one withdrawn and examined with a lens, and whenever a suspicious looking speck was observed the glass was put in a pail of sea-water and taken to the station to be examined with a compound microscope.

---

[3] Ryder, Comm. Fish. Maryland, 1881, p. 57; Bull. U. S. Fish Comm., 1882 (1883), p. 383. Horst, Bull. U. S. Fish Comm., 1882 (1883), p. 165; Rep. U. S. Fish Comm., 1884 (1886), p. 906. Möbius, *Zool. Anz.*, Jan. 22, 1883. Winslow, Bull. U. S. Fish Comm., 1884, p. 354. Jackson, *Science*, 1888, p. 230 (Vol. XI, No. 275); *Mem. Bost. Soc. Nat. Hist.*, 1890, p. 285.

The strips soon became dirty, receiving a slimy coat speckled with sediment, plants and animals. There were bacteria, diatoms, algæ, protozoa, sponge-spicules, hydroids, polyzoon-colonies, worm-larvæ, crustacean larvæ, small snails, etc. It seemed as if everything but oysters could be obtained. So far as I saw, I had neglected nothing that might contribute to the result in view. Could it be that my suspected larvæ were not oysters, that there were no oyster larvæ or oyster eggs in the water! Once more I was bewildered.

At length, on the sixteenth of August, I discovered a single minute oyster-spat, bearing unmistakable marks of recognition and enclosing within the lately deposited spat-shell the prodissoconch of the free-swimming larva. On the nineteenth I found a second (Fig. 3), and on the twenty-second a third (Fig. 1). Everything speedily became clear. My experiments had been running ahead of nature. Oyster larvæ had been in the water, but they were not ready to transform into spat. They had to wait their time. On the thirty-first of August a fourth was taken.

After finding the first oyster-spat on glass I at once directed increased attention to natural marine objects and on the second of September I found a spat on the surface of a half-grown oyster-shell. From this time forwards they were to be found in increasing numbers and on various objects and, after being once shown them, the deck-hands of the steamer *Ostrea* could also find them. I have found spat on the shells of the oyster, mussel, clam, quohog, bar-clam, razor-clam, round whelk and on stones, but they must occur on many other objects as well. Judging from the numbers of half-grown oysters that carry periwinkle-shells at their umbos, it would seem that the periwinkle is a common base of fixation, although I did not succeed in finding any with young spat attached. The dark color of the winkle, of course, makes it easy to overlook the smallest spat, and besides, these shells are frequently speckled or spotted with plant colonies such as *Ralfsia verruscosa,* the small colonies of which may simulate young oyster-spat in size, shape and color. One can distinguish the difference with a lens or by feeling them with a knife-blade. The young of *Crepidula formicata,* a low conical-shelled gastropod, is sometimes more difficult to distinguish, but with a knife-blade one can slide it along the base of attachment or pry it off and note that there is no under shell but a broad clinging and creeping foot. Anomia is one of the closest relatives of the oyster, but, from its shape and color, is usually not difficult to distinguish. Upon prying it off, the thin lower valve of the shell can be seen to have a hole through which a short stalk of attachment passes and permits movement. The oyster becomes fixed by means of a secretion, presumably from the edge of the mantle, which cements the left valve close and fast to the supporting rock or shell.

The spat caught on glass did not, of course, occur in regular order of progression in size: the first measured .87 × 1.03 mm. in height and length, the second 1.58 × 1.20, the third .51 × .55, the fourth .86 × .95. Similarly the first found on an oyster shell measured 2.4 × 2.3, while those subsequently procured varied from less than 1 mm. to 6 mm. in height.

The shell of the larva is longer than high, and this is true not only for each valve but also for the whole shell, even when the far umbo, through tilting of the shell, stands up above the near one. The youngest spat agree also with this statement, but when about 1 mm. in height the proportions become reversed, and from this time forwards the shell grows fastest below and at the postero-inferior angle. On this account it is more useful at first to build comparative measurements on the height rather than on the length—the height, both for the larva and for the spat, being the vertical measurement from the top of the umbo to the lowest level of the opposite edge when the prodissoconch is placed in the position of a creeping clam.

The spat caught on glass exhibited the characteristic color of the pelagic larva—the smallest varying towards pink, the larger towards brown. Those taken on opaque objects, on the other hand, presented a different appearance—instead of having a pink, reddish or brown coloration as one would expect from comparison with the larva, or, instead of having a white appearance as might be looked for by comparison with the older spat and adult oysters, they preserved a shining, dark, metallic lustre with a few faint radial lines. In the center of the dorsal region could be distinctly recognized the larval shell (prodissoconch) of the oldest free-swimming stage, presenting a uniformity of appearance in all the specimens, and measuring in the neighborhood of .369 × .384 mm. in height and length.

The spat-shell (young dissoconch) is deposited by the thickened rim of the mantle in layers along the ventral and terminal edges of the larval valves, but not to any extent along the dorsal or hinge edge, which explains the concentric lines below the umbos. The latest deposited parts around the margins are very thin and delicate and exhibit a prismatic structure. At first the shape varies little from that of the prodissoconch, but soon the dissoconch becomes extended fore and aft of the hinge-area in a manner that suggests the wings (ears) of a scallop-shell, the lower parts preserving a pretty uniformly curved outline. Later these alæ cease to be conspicuous and the whole outline may become irregular and variable. Deep or shallow concentric creases preserve more or less indication of stages of growth, and at places may be portions of radial lines. The deeper concavity of the left valve remains noticeable for a time after fixation takes place, particularly in sections, but a little later the lower valve seems to lag behind the upper one in growth, appearing thinner and flatter, while the upper one is thicker and more curved. At a still later period the growing edge of the lower valve becomes free and the valve again acquires a deeper cavity than the upper one, preserving this difference throughout life.

While the developing oyster is free to swim or to creep it is, of course, natural to describe it in terms suitable to such permanently free-living species as the clam. The more pointed end, that ordinarily precedes in locomotion and from which may protrude the velum or the foot, is the anterior end. The foot is postero-ventral to the velum. The umbos are postero-dorsal. The hinge is dorsal, *i. e.,* between and in front of the umbos. The longest diameter is horizontal, and the height is a vertical line at right angles to the length. With the growth of the spat it becomes difficult to retain such ideals as continuously useful marks of description. At periods varying somewhat with the individual they become more or less modified. Preserving the original orientation of the prodissoconch, the height of the dissoconch soon becomes greater than the length, the hinge and umbos come to mark the narrow anterior end of the spat, and the larval shell sinks into insignificance. Its left valve frequently becomes obliterated by growth of the surface of attachment, but its right valve may often be found until late in the life of the spat, although it is liable to become destroyed by weathering of the umbo-region. While its position marks the anterior end of the oyster, it has long since been carried up on the tip of the umbo of the dissoconch out of reach of the hinge or of the growing parts, but its anterior end still points in a general way in the direction of the anterior end of the adult. This position and relationship is correlated, as will be seen later, with the increase of growth of the lower and posterior parts of the oyster's body, which occasions more or less of a rotation round the great adductor muscle, and resulting in longer or rounder forms of shell with a straighter dorsal and a much curved ventral border.

The right, upper, valve remains flatter and smoother, the left, lower or attached valve, more deeply hollowed, rougher, with more conspicuous concentric furrows, and often with blue tipped projecting processes.

Note on the Asymmetry of the Shell.—In the free-swimming larva the greater convexity of the left valve can not be due to external conditions in the life of the larva since both valves are developed under like conditions, but must result from a cænogenetic modification of biogenesis, which is to say that the difference in the two valves was first developed after some remote but free and symmetrical ancestors of the present oyster took to a fixed mode of life, becoming attached by simply cementing the left valve fast to a solid substance upon which it rested, and that somewhat later in the phylogenetic development the hereditary transmission of this character became modified to precede, in the life of the individual, the conditions which originally called it into existence. It is conceivable that gravity was the prime incentive both to the occasion for fixation on one side and to the first asymmetry. Many other mollusks have been similarly modified, *e. g.*, Anomia, Pecten, Mya, deep-bodied animals that habitually fall over on one side as soon as locomotion ceases. When once developed there may have been an advantage in transmitting the lob-sidedness to earlier and earlier stages in the offspring, which could take place by natural selection. Such an advantage might well be the determining that the heavier left side of the larva, when settling to the bottom or when creeping movement ceases, should promptly come in contact with the point of fixation and insure the most favourable relative positions for the activity of other organs whose function had been perfected under like conditions in the adult. The temporary transfer of the greater convexity to the upper valve in young stages of the spat can be explained by the fact that for a time the growth of the lower valve follows, as it is cemented to, the surface upon which it rests, while the upper valve is free for growth in every direction. When a sufficient surface of attachment is secured the edge of the lower valve becomes free, and then the greater convexity soon reverts to the left valve again.

In living spat the mantle can be often seen protruding beyond the edge of the shell, but in preserved specimens it is retracted, sometimes close up to the gills and body, so that the soft parts of the animal may occupy only a half to a third of the cavity of the shell. In the youngest stages the margin of the mantle is thickened, and the beginnings of tentacular processes are present. Differences in the two sides afterwards become noticeable, such as thickness, length, and the greater freedom of the right side from the body, where, for a considerable area in front of the adductor muscle, there is open communication from the supra-branchial chamber to the outside at the dorsal edge of the shell (Figs. 14, 15).

The anterior adductor muscle is present for a time in the spat, and appears to move upwards and backwards from its original position in the larva, until it is crowded to the edge and disappears before the oyster reaches 1 mm. in depth. The posterior adductor muscle, on the other hand, increases regularly in size and moves downwards and slightly backwards, leaving distinct lines on the shell to indicate its change of position. In spat .86 mm. high it is just below the edge of the prodissoconch (Fig. 2), in those 1.5 mm. high it is twice the depth of the prodissoconch from the top of the shell (Fig. 3); in all stages it is nearly in the median horizontal plane and slightly posterior to the median frontal plane. The movement may be effected by a slow creeping of the muscle, due to downward pressure from the growth of the body above, or by the addition of new fibers below and the absorption of old from above, while the impressions on the shell may result from the inability of the mantle to deposit new layers of pearly matter under the attached ends of the muscle.

Of the organs enclosed by the mantle a conspicuous part is early assumed by the gills. The oldest larva or the youngest spat has two of these—one on each side of the body, below and between the line of attachment of the mantle and the base of the foot. At this time each gill possesses a row of about eight filaments, of which the anterior are larger and more completely separated from each other, the posterior are shorter and only partly separated by vertical creases, while all are united above by an undivided longitudinal ridge or basal axis that projects behind and below the mass of the body. At the time of fixation the right and left gills are approximately equal, but when the spat reaches .86 mm. in height (Fig.

2) there are about sixteen long filaments on the left side and about ten short filaments on the right side—the left gill extending in front of and behind the right one and occupying most of the gill-chamber (Figs. 4–8). In spat of 2.5 mm. height there appears on the right side, outwards from the already present gill, a third series of minute, papilla-like filaments (Fig. 14), and when the spat reaches 3 mm. in height a fourth series is to be seen in the corresponding position on the left side (Fig. 15). They increase in size during the growth of the spat until the animal possesses four complete gill-leaves corresponding with those of the adult.

During larval development the gills of the oyster make but little progress towards the complicated structure of the adult. The free-swimming animal being small, respiration can for a time be partly subserved by its surface. But fixation effects a marked change in its mode of life and is followed by far-reaching modifications in its organization. Rapid increase of size demands improved facilities for respiration. But, as the animal no longer comes in contact with its food through swimming movements, it must depend upon the respiratory currents for bringing food to itself; hence the gills acquire a double importance. Moreover, since the conditions favorable to bilateral symmetry are interfered with, the equal balancing of right and left sides in the further growth of organs must be left to heredity. At the time of fixation, as we have seen, the gills are represented by two bilaterally symmetrical inner gill-leaves. The left (now under one) grows much faster than the right (now upper one) so that there is more room and less pressure above, facilitating the development of the right outer gill-leaf before the corresponding one of the left side. Irregularity also soon becomes noticeable in the higher level of origin of those of the right side and in a tendency towards a radial symmetry of the organs with reference to the posterior adductor muscle.

A study of sections of larvæ and young spat reveals a remarkable difference in the apparent ontogenetic development of the gills of the oyster as compared with the recorded phylogenetic development in lamellibranchs. This, like the larval asymmetry of the shell, may be understood as a short-cut towards the final structure. As the first-formed, short, basal axes grow backwards they carry with them a continuation of the body-wall, connecting them with one another across the median sagittal plane and with the mantle at both sides, giving rise to a very imperfect separation into branchial and supra-branchial (or cloacal) chambers. The filaments are at first short, solid, papilla-like outgrowths from the axes —the older and larger anterior, the younger and smaller posterior. They originate behind, but by formation and growth of new ones those first formed become pushed forwards. The at first small and shallow supra-branchial chamber follows this movement and penetrates each filament from above, distending it laterally but not antero-posteriorly because of the pressure of contiguous filaments. This process continues until each filament is severed into an outer and an inner section, the intermediate portion becoming constricted through, but never completely at the tip. In this manner each gill-leaf becomes split into outer and inner lamellæ of similar structure, but the one the reverse of the other, with its parallel half-filaments and intervening slits overhung by cilia. Imperfect separation of the transverse median portions of the opposed halves of some filaments gives rise to the inter-lamellar junctions, while the imperfect separation of the opposed sides of different but contiguous filaments occasions the inter-filamentar junctions. The same process can be observed later in the development of the right and left outer gill-leaves as well as in the terminal filaments of any one of the four (Fig. 14).

For a long time it has been customary among zoologists to speak as if the oyster, or other bivalve mollusk, possesses four gills, which it really appears to do, two on each side of the body. Comparative study of the anatomy and of the development of different groups has led to the view that bivalves have been developed from primitive, symmetrical, gastropod-like ancestors, with a simple head in front bearing two tentacles, two eyes, and mouth with a rasping tongue; a low conical shell above that could be drawn down over all the soft parts and lined by a mantle that secretes its material; a flat creeping and clinging foot below; and two feather-shaped gills, disposed right and left, projecting backwards. Each of these was a symmetrically constructed, bipectinate gill or ctenidium, having a central axis with two rows of filaments, an upper and a lower. There are still living limpet-like gastropods along our coasts possessing such characters, although no one species retains them all or in the most primitive form.

The group of mollusca to which the oyster belongs has in the course of time suffered modifications of the characters mentioned. Its members have taken to a more quiescent mode of life, such as burrowing in sand or fixing to rocks, and in consequence have largely lost those external organs of locomotion, plunder and special sense so necessary to free-roving animals. The absence of a head has been regarded as characteristic (hence the group has been called Acephala); in place of a single piece they have developed a shell with two valves (Bivalva); the foot in by far the greatest number of forms has become somewhat hatchet-shaped (Pelecypoda); the gills are leaf-like, each separable into flat plates (Lamellibranchia). If all bivalves had become equally modified it would certainly have been difficult to determine the origin of the group, but, owing to the diversity of natural conditions and the reactions of these upon living organisms, certain species have been forced to pursue special lines of action in order to better their chances for life, with the result that the organs chiefly concerned have become more specialized, while other organs have retained much of their original structure, and it is just these organs that are especially valuable in tracing ancestral affinities. As long ago as 1848 Leuckart (16) comprehended the essential unity of molluscan gills, and his views have been supported by Menegaux, Pelseneer, and many others. Peck has studied the Lamellibranch gill. Lankester, Hatschek, Thiele, Lang, are among those who have studied the phylogeny.

In the oyster larva one can at once recognize the ctenidial axis with its lower series of filaments, but one has to await the spat of 2.5 to 3 mm. before he can see the upper series, which has had to rotate outwards nearly half way round the axis in order to remain accommodated in the branchial chamber. In the adult there is but one gill on each side, comparable with a gastropod ctenidium and composed of two hemibranchs (gill-leaves or branchial foliæ); each hemibranch may be split lengthwise, from above nearly to the lower free edge but not through it, into outer and inner plates (lamellæ), or subdivided transversely into numerous V-shaped branchial filaments of which one half belongs to the outer lamella and the other half to the inner lamella of a hemibranch.

In the course of phylogenetic development the originally straight filaments have become bent upon themselves to permit of greater length (surface) and still be protected within the branchial chamber—those of the ventral series were folded inwards and those of the dorsal (but now lateral) series were folded outwards, while the tips coming in contact with the foot in the one case or the mantle in the other clung for support, were directed upwards, and finally became fixed along the side of the body or along the inner surface of the mantle. At places their ciliated surfaces became knit together for further support, leaving intervening gill-slits between contiguous filaments, and ascending water-tubes between opposite lamellæ. At the level of union of the gills with the body and with the mantle there is separated off a branchial chamber below from a supra-branchial (or cloacal) chamber above, and by the activity of the cilia water is brought into the former, directed through the gill slits, up the water-tubes, and out by the cloacal chamber. The original ctenidial axis lies above the base of origin of each pair of hemibranchs, and is marked by retaining its connection with the body by a septum carrying blood vessels and nerves (Fig. 17).

Two larval organs soon disappear under the new conditions brought about by fixation: the velum and the foot. Even in certain old, free-swimming larvæ, that are perhaps belated in their efforts to become attached, a reduction in the size and vigor of the velum is noticeable. This would seem to suggest an atrophy of the organ, which might be followed by either dehiscence or absorption. I have occasionally seen old larvæ with the velum protruded and partly severed from the body, as well as completely separated vela still capable of muscular and ciliary movements. Such cases may have resulted from accidental pinching off by a snapping closure of the shell-valves. But the size, appearance, enfeebled movements, and even the accident itself, pointed towards an antecedent loss of ability to respond correlatively to the activity of neighboring organs.

Balfour (21, p. 215) states: "It has been suggested by Lovén, though without any direct evidence, that the labial tentacles of adult Lamellibranchiata are the remains of the velum. The velar area is in any case the only representative of the head."

Ryder (31, p. 404) says: "The detachment of the ring or crown of vibratory filaments or cilia from the embryo as asserted by Davaine has not been confirmed by any other observer" and in 8, p. 790: "Davaine makes the statement that the velum appears to drop off sometime about the end of the larval period. Gerbe, on the other hand, asserts that the velum is transformed into the palps." This is a fascinating view of the destiny of the velum: that it does not become entirely useless and completely disappear, that its main line of folding in the median sagittal plane represents the division into two halves which bend around the sides of the mouth, each half again folding to form the two palps, while secondary radial foldings may give rise to the furrows and ridges and the cilia become redistributed. On the other hand it is not easy to see exactly how an organ of the size and shape of the velum could become reduced, remodelled, changed in position and folded in such a way as to form an anterior pair of palps, connected across in front of the mouth, and a posterior pair, connected behind the mouth and underlying the first, while the two on one side are attached along a line running back from the mouth and have their original ciliated surfaces turned towards each other. Moreover, this would mean a much more intimate connection between the epithelium of the velum and the inner walls of the mouth than exists in the larva, where the mouth-opening is surrounded by a funnel-shaped projecting rim, that is separated from the velum in front by a crease, while the lower lip is free to a still greater extent. There is no observable connection between the arrangement of cilia on the velum and on the palps, nor any positive antecedents of the furrows and ridges of the palps on the velum. Besides, from a consideration of the size of the velum in the larva and the size of the smallest recognizable palps in the spat, it would appear that the velum would have to suffer a period of decay followed by a period of vigorous growth. Restricting one's observations to the oyster it might seem just as likely that the lower palps should originate from the foot and only the upper ones from the velum. The foot is ciliated and has a median ventral furrow corresponding with the division-line between the lower palps. In that case one would expect to find vestiges of pedal organs, such as pedal ganglia and otocysts, about the bases of these palps under the œsophagus, as well as supra-œsophageal ganglia in the bases of the upper palps in front of the œsophagus. But in my sections I have not been able to recognize these structures, and reflection on other bivalves, where both foot and palps persist as functional organs in the adults, proves beyond doubt that the foot has nothing to do with the lower palps. I have three series of young spat-oysters with the shell measuring rather less than 1 mm. in height, and from a study of them I should say that the palps originate from, and belong to, the walls of the mouth, *i. e.*, are extended upper and lower lips.

The foot, after fixation of the larva, no doubt ceases to grow, perhaps becomes reduced, but in any case shrinks against, is absorbed into and incorporated with the anterior ventral wall of the rapidly enlarging abdomen. In 1 mm. spat it is scarcely recognizable as a median, grooved, muscular thickening between the lower lip and the first gill-filaments.

Jackson (12, p. 303): "The fact that a velum, or swimming organ, exists up to the period of permanent fixation accounts for the great reduction of the foot, because that organ is unnecessary while the animal is provided with another locomotive organ, and is useless for progression after the animal is attached. The reduction of the foot is clearly attributable to disuse and a high degree of concentration of development . . . seen so markedly in the development of the oyster." I have already shown, when dealing with the foot of the larva, that the part designated "foot" by Jackson and others is not the real foot, which is only to be found at a very much later period and which they had not recognized.

The intestinal system has all its parts represented in the larva. With the growth of the spat these suffer certain alterations in relative sizes, shapes, and positions. Perhaps the most radical change is produced by a rotation of the body in such a way that the mouth moves forwards and upwards towards the antero-dorsal margin of the prodissoconch. This doubtless accompanies and is associated with the loss of the velum, which in the larva is so large as to occupy all the fore part of the cavity of the shell, forcing the mouth and œsophagus backwards to near the median frontal plane of the body. In spat under 1 mm. in height when the velum is completely cleared away, the mouth can occupy its normal position as in the adult. Such a rotation may appear at first thought inexplicable, but when it is remembered that in the prodissoconch the body of the larva is possessed of great freedom of movement, being at times thrust far forwards, putting the retractor muscles on the stretch, it can be readily understood. In fact it is conceivable that these muscles may be made to do duty in producing the rotation and in fixing the body in its new position, for after the loss of velum and foot there is no longer any need of such free movement, consequently these muscles may lag behind other parts in growth, exerting a tension as they do so sufficient to cause the rotation. In harmony with this view is the similar upward movement of the anterior adductor muscle and the rapid downward movement of the posterior adductor muscle.

In 1 mm. spat the two sides of the mantle, meeting above at a broad angle, appear to be suddenly thickened (Fig. 4) into a sort of upper lip for the widely open, transversely crescentic mouth, that opens a little farther back on the right side than on the left. The anterior end of the body, between the first gill filaments, serves as lower lip, while very short upper and lower palps, possessing only a couple of ridges and furrows, are continuous with the lateral margins of the upper and lower lips, and project on each side of the anterior end of the median left gill. In 2 mm. spat (Fig. 13) the palps have increased perceptibly, doubled the number of furrows, turned down, and are seen to be anterior to, but not continuous with, the gills. Judging from the great progress made between these two sizes, I believe that the palps originate sometime before the spat reaches 1 mm. in height, but are not present as such in the larva, where upper and lower lips and palps are represented by the internally-ciliated, funnel-like, projecting rim of the mouth. When this rotates upwards it comes to lie between the mantle above and the forward growth of the abdomen below, while its side-angles fold outwards and backwards becoming the palps, their like surfaces turned towards each other and their cilia continuous with that of the mouth and œsophagus. Later they become adherent to a greater extent along the lateral walls of the anterior part of the enlarging abdomen, and direct food from the gills into the mouth.

Rice (33, p. 28) curiously made the observation: " During the first period of attachment when the shell itself is not firmly attached, but simply held firmly down to the substance with which it is in contact,

> the young animal gets its food, or a portion of it, by means of a sort of proboscis, or elongation of the mouth part, which is capable of being moved about freely within the shell cavity. This proboscis stage lasts until the gills are fully formed and becomes of sufficient size to supply food to the animal, when the proboscis, or rather its flexible end, is transformed into the labial palps which become closely connected with the gill-leaves."

The mouth narrows down into an œsophageal tube of transversely elliptical calibre, lined by cells similar to those of the mouth. It is still relatively long and curves over the anterior end of the stomach, passes between the lateral origins of the liver, and enters the stomach from above (Figs. 2–10). The stomach is a relatively large mass of irregular shape and large cavity, occupying a good part of the space in the prodissoconch. There may be considered to be three prominent extensions: one forwards below the œsophagus, another postero-dorsal behind the entrance of the œsophagus, and a third, beginning as a compressed ventral extension of the first, slants downwards and backwards towards the adductor muscle, becoming broad, deep, regular and thick-walled. This, I am satisfied, is the portion that secretes the crystalline style, and originates postero-dorsally in the left umbo of the larva, but becomes moved to its present position during the rotation of the viscera, and presents the appearance of being internally ciliated. Just in front of the insertion of the œsophagus but on each side of it, *i. e.*, dorso-laterally, spring the stalks of the liver—one on the left and two on the right. These branch into numerous follicles lying on both sides of and above the stomach and projecting far forwards to the region of the mouth. On the ventral aspect of the stomach, in the same region, springs the intestine, on the right, in the crease between the compressed antero-ventral extension to the left and the main central body of the stomach above (Fig. 9). From this the intestine passes backwards on the right, then upwards behind the rounded postero-dorsal extension, forwards and down the left side, where, near the anterior end of the stomach it turns backwards and then down, finally passing towards the median plane to the anal opening over the adductor muscle. The stomach sometimes contains diatoms and desmid-like clusters of one to four nucleated cells.

The nervous, circulatory, excretory and reproductive systems remain undescribed, and shall not be treated of in this paper; they bear less important relations to those characters of external morphology and gross anatomy that are so useful as marks of recognition and description.

The first, second and third spat oysters caught on glass were of different sizes and were consequently devoted to morphology, but the fourth, being of approximately the same size as the first, was used for a physiological experiment in growth. This spat was procured on the afternoon of August 31 at Ram Island, about six miles from the station, and measured at 5 P.M. .861 × .953 mm. in height and length and had about sixteen gill filaments. It was kept under the bridge of Keir's wharf until the afternoon of September 1 and measured again, but it showed no increase of size. It was then taken to Ram Island and placed under its original conditions in a crock, and at 4 P.M., September 7, it measured 1.276 × 1.261 mm. and had about twenty-four gill filaments. It was kept in running seawater until 5 P.M. of the eighth and then put under the bridge of the wharf until the morning of the ninth, when it was again taken to Ram Island. It did not grow either in the running water or under the bridge where there is at times considerable tidal current. On the forenoon of the sixteenth it was again brought in and measured 1.753 × 1.661 mm. From these observations it would appear that the young spat did not become immediately accommodated to new conditions after being disturbed, that during a period of six days of undisturbed growth it increased to one and one half times its original height, and that at the end of seven days more it had grown to twice its original height. One might say that it doubled its height and length in two weeks.

Having to leave for Montreal by the twentieth, it appeared that the best thing left for me to do was to plan an experiment for the winter. I had three strong wire baskets made—two feet square by three inches deep and lids to fasten over—in which I placed perhaps three to four hundred small, selected, living oysters having one or more minute dark spat upon each shell, surrounded with circular lead-pencil marks for convenience in recognition. These baskets were connected by a long rope and put down in a deep channel between Hog and Bird Islands, presumably out of the way of fishermen, ice-shoves, etc. I expected the small dark spat, which varied from 1 to 4 mm. in height, to grow to about the size of one's thumb-nail during the winter and spring, as this was the size of the smallest white spat I recollected having seen upon first arriving at Malpeque the previous spring. The first thing I did the succeeding spring was to go and grapple for these baskets, but despite every effort they could not be found. The marks of the rope and baskets could be observed on the bottom, and the suspicion was near that some curious fisherman, in setting lobster traps in the early spring, had found them and taken possession for the rope—an illustration of the immediate short-sighted petty-selfishness and improvident disregard of impending wholesale benefits of many fishermen.

The next thing that suggested itself was to look for spat of the previous autumn on the shells where I collected those for the preceding experiment, and I was surprised to find dark spat still there, that had apparently not grown a bit or changed in color during the winter. There were fewer of them—many having died and lost the upper valve or even both valves were gone, leaving sometimes a patch or rim to indicate where a spat had been attached. The largest dark spat collected the previous autumn measured 6 mm., and the largest found the next spring was 8 mm. in height. They retained their dark metallic luster with radiating ridges or lines and very thin edges—the whole oyster being thin and fitting so solidly against the supporting shell as to require some force with a knife-blade to separate it. In some of the larger was to be seen a tendency to turn white, in that the dark rays were irregularly separated by reversed lighter radiations. Sizes but little larger than these may be found later in the spring and in the early summer. The spat of the oyster-fishermen, varying mostly over one inch in length, are abundant, many barrels of which are collected by the Indians at Ram Island Point and thrown out off Lennox Island, the Indian reserve, for further growth.

Important results added to those given in the preceding part on the larva are:

19. First systematic use of plankton nets in the procuring of oyster larvæ.

20. First undoubted recognition of the larva of the oyster in Canada.

21. Stages hitherto unobserved (constituting the blank referred to by Jackson) may be taken in the plankton net.

22. The first undoubted recognition of young stages of Canadian oyster spat.

23. The spatting period has been limited.

24. The free-swimming period of life of the larva has been limited.

25. Size is a more useful criterion than age.

26. Sections have been prepared of both larvæ and spat in order to determine accuracy of structure.

27. The gills have been carefully studied.

28. The intestinal system has been described throughout.

29. Development has been followed up to adult sizes.

30. Many structural or other observations have been made, which to enumerate would be largely to rewrite foregoing pages.

ADDITIONAL SELECTED LITERATURE

16. 1848. Leuckart. Ueber die Morphologie und Verwandtschaftsverhältnisse der Wirbellosen Thiere. Braunschweig.
17. 1849. Lovén. *Arch. f. Naturg.* (and *Ann. Mag. Nat. His.*, 1856).
18. 1853. Davaine. *Comp. Rend. et Mèm. de la Soc. de Biol. Paris,* IV, p. 295–339.
19. 1876. Gerbe. *Zool. Record,* XII, Mol. 62.
20. 1877. Peck. The Structure of the Lamellibranch Gill. *Quar. Jour. Micros. Sci.,* XVII, pp. 46–66.
21. 1880. Balfour. A Treatise on Comparative Embryology, p. 215.
22. 1883. Lankester. Encycl. Brit. (article Mollusca).
23. 1888–91. Hatschek. Lehrbuch der Zoologie.
24. 1888–89. Menegaux. Sur la branchie chez les Lamellibranches. *Bull. Soc. Philom. Paris.*
25. 1889. Pelseneer. Sur la class. phylog. des Pélécypodes. *Bull. Soc. France et Belgique.* Contrib. à l'étude des Lamell. *Arch. Biol.,* 1891.
26. 1891. Thiele. Die Stammesverwandtschaft der Mollusken. *Jena. Zeit. f. Naturg.*
27. 1896. Lang. Text-book of Comparative Anatomy, II.
28. 1900. Korschelt and Heider. Text-book of Embryology of Invertebrates, IV.
29. 1878. Winslow. Extracts from Report of Investigations of the Oyster Beds in Tangier and Pokamoke Sounds and Parts of Chesapeake Bay.
30. 1884. Winslow. Bull. U. S. Fish Com., pp. 234, 468–9.
31. 1882. Ryder. Bull. U. S. Fish Com., pp. 403–19.
32. 1883. Ryder. Bull. U. S. Fish. Com., pp. 281–294.
33. 1883. Rice. Experiments in Oyster Propagation, *Forest and Stream,* N. Y., Aug. 9, XXI, pp. 28–29.
34. 1885. Rice. The Prop. and Nat. His. of the Amer. Oyster. Rep. Com. Fish. State of New York. Albany, pp. 71–137.
35. 1880. Brooks. *Proc. Bos. Soc.,* XX, p. 325.
36. 1905. Brooks. The Oyster. Baltimore, pp. 1–225.
37. 1890. Jackson. Studies of Pelecypoda. *Amer. Nat.,* XXV, pp. 1132–1142.
38. 1891. Jackson. The Mechanical Origin of Structure in Pelecypoda. *Amer. Nat.,* pp. 11–21.
39. 1900–1907. Nelson. Reports of the Biol. Dept. of the New Jersey Agric. Coll. Exper. Sta.
40. 1874. Whiteaves. Notes on the Marine Fisheries, etc. Appen. U, pp. 18–29. 6th Ann. Rep. Dept. Mar. and Fish., Ottawa.
41. 1889. Ganong. Economic Mollusca of Acadia.
42. 1899. Kemp. Report on Can. Oys. Fish and Oys. Cult., 31st Ann. Rep. Dept. Mar. and Fish., Ottawa, pp. 259–359.

BRIEF NOTES AND EXTRACTS

Ryder (I. The Larva. Literature, No. 6, f. 3) and Jackson (No. 12, ff. 1, 2, 17, 18) have given figures of the youngest stages of oyster spat.

In the absence from the literature of any figures of the oldest free-swimming larvæ, I have already referred to these and for a more satisfactory understanding reduced their measurements to actual sizes. They represent the spat within 24 hours after fixation and measure in the neighborhood of .3 mm. in height. Ryder's Figs. 5, 4, 6, 7, represent spat of about .34, .38, .51, .54 mm. height. Jackson's Fig. 3 was perhaps about .55 mm. high and his Figs. 20, 21, about .91 mm. high. Then come Ryder's Fig. 8, about 1.6 mm., his (No. 8, p. 784) Fig. 2 of 3 mm., and Jackson's Fig. 4 of 5 mm. My youngest spat were .51 and .86 mm. high and from 1 mm. upwards I had such abundance I could select whatever sizes I desired.

On account of recorded differences between European and American oysters it is not always safe for us to judge from analogies. On the other hand, except for local differences of temperature, food, fauna, etc., the accrued knowledge of oysters in the United States is of immense value to Canada.

Importance of Embryological Study.—Winslow (No. 30, p. 234): "I would press the importance of continued investigation of the embryological life of the oyster. The effects of the various influences to which it and the mature animal are exposed should be determined as early as possible. Knowledge of these influences and intelligent appreciation of their effects are absolutely necessary to the success of oyster culture. Thousands of dollars would be annually saved to the Connecticut oystermen if they could determine, with even approximate accuracy, the date when the attachment of the young oyster would occur. Hundreds of thousands would be saved if they had any reliable method of determining the probabilities of the spawning season. Careful, continuous, and elaborate study and investigation alone can determine these points and others of equal importance. Considering the value of successful determination, not only in a scientific aspect, but practically, no effort or expense should be spared to obtain it."

Spawning.—Winslow (29, p. 130), Tangier and Pokamoke Sounds: "The spawning season was said to be from May until August inclusive, though most of the spawning was done in June and July." Brooks (5, p. 10): "Oysters in from 1 to 6 feet of water in the vicinity of Crisfield, probably spawn between the middle and end of May, but oysters with ripe eggs were found in water from 5 to 6 fathoms deep from the first to the thirtieth of July, although most of them spawn late in June." Ryder (7, p. 326): "In the region of the Chesapeake the most important spawning period seems to extend over the months of June and July, but considerable ripe spawn may be found even much earlier and later than this."

Growth of Larva.—Ryder (7, p. 328): "At a temperature of 75 to 80° F. the period of incubation of the American oyster is only 5 to 6 hours, when the young commences to live an independent active existence." "The duration of the locomotive stage of development of the larva has not yet been certainly determined . . . it has been found by the writer that under favorable circumstances attachment of the fry probably takes place within 24 hours after fertilization as represented at *m* in Fig. 1. The young, however, after attachment, continue to grow as larvæ . . . when the valves of the fry have acquired umbos the development of the spat shell begins." Ryder (9, p. 728): "I would infer from what we learn from the study of other animals that it may require quite a week before an embryo reaches the dimensions of 1/80 of an inch, but we have no data upon which to base any conclusions of value.''

Spatting.—Rice (34, p. 115): '' The attachment takes place in about two days from the time of fertilization.'' Jackson (11, p. 532): ''One of the most successful spatting grounds at Buzzards Bay is a sand spit on South Wareham . . . oysters were spatting most abundantly late in July and early August.''

Growth of Spat.—Ryder (9, p. 728): ''After fixation the growth of spat is very rapid—week or 10 dys., ¼ inch across; 20 dys., $\frac{7}{16}$ in.; 44 dys., $\frac{13}{16}$ in.; 48 dys., 1 in.; 79 dys., 1¾ in.; 82 dys., 2 in.'' Ryder (7, p. 328), Figs. 5, 6, 7, etc.

Number of Spat.—Ryder (32, p. 287): ''As many as 25 young oysters might have been counted on a surface of one square inch'' on wooden buoys taken up early in July near Woods Holl. ''More than 100 oysters on a single shell.'' Rice (34, pl. 6, f. 12) figures the inside of an old oyster valve with 165 young attached. I never saw anything like such numbers at Malpeque—having to examine many shells to find one bearing one or two spat.

Output.—Winslow (30, p. 233) gives for the United States 22,195,370 bushels, of which 19,712,320 bushels came from Chesapeake and Delaware Bays. Kemp (42, p. 353) gives for Canada a table from which it is seen the maximum production was reached in 1882 of 64,646 barrels.

Breeding.—Rice (34, p. 115): ''The first efforts in this country in the direction of artificial propagation were made by the writer in the summer of 1878 in conjunction with Dr. W. K. Brooks, but these experiments were not successful. The next summer, however, Dr. Brooks succeeded in impregnating the eggs and in raising the embryos until they were six days old.'' Brooks (5, p. 3): ''. . . succeeded in raising countless millions of young oysters.''

Oyster Culture.—Under this head might be included an extensive literature dealing largely with the transplanting of oyster spat, that have escaped the accidents of nature, to more favorable localities as regards crowding, competition, food, cleanliness, etc.; but also to a more limited extent the breeding of larval oysters under artificial conditions that protect them against extremes of temperature, violent storms, starvation, rapacity of animals, etc., and the furnishing of abundant and suitable objects for fixation. The subject is too vast for discussion in this place.

It would appear that, to some extent simulating the life-history of the oyster, the short period of activity in investigation and experimentation initiated by Brooks was succeeded by a period of quiescence in research, when statements were repeated but not examined anew. Deliberate, painstaking, self-reliant, and unbiased work, like that of Nelson (37), may do much to originate a new cycle of exact observation, which sooner or later may be turned to account in a rational system of oyster culture.

Montreal, May 18, 1909.

THE ALIMENTARY CANAL OF A CARBONIFEROUS SALAMANDER

DR. ROY L. MOODIE

THE UNIVERSITY OF KANSAS

INVESTIGATORS, during the progress of their research into the anatomy of extinct animals, have the good fortune, from time to time, to be able to add items of interest to the soft anatomy of the forms which they are studying. In the nature of the case the soft parts are very rarely preserved and when they are represented it is usually an imperfect record. Occasionally, however, the rocks yield forms which afford very complete knowledge of the soft anatomy of the animal. This has been strikingly shown in Dr. Dean's studies on the fossil sharks of the Cleveland shales of Ohio. Dr. Eastman and Dr. Parker have also studied and described the soft parts of the head, especially, of a peculiar little fish from the Waverly shales of Kentucky which Dr. Eastman has named *Rhadinichthys deani.* In this species, which is represented by an abundance of material, there are clearly preserved the various portions of the internal ear, the outlines of the lobes of the brain and traces of an arterial blood vessel with some of its branches. There are many other instances in which the soft anatomy of fossil fishes has been developed. Many of these are given more at length by the writer in another place.

Among the higher vertebrates the softer structures are not so well known. The outlines of various branchiosaurians are known from the studies of Fritsch, Credner, von Ammon, von Meyer and Thevenin, who have described these forms from the Permian and Carboniferous of France, Bohemia and Germany. Cope has dwelt at some length upon the preservation of the shape and some of the coloring matter of the eye of the reptile-like microsaurian, *Amphibamus grandiceps*, from the Mazon Creek shales of Illinois. The writer has been fortunate in observing the outline of the body of this species. He has also observed muscle fibers in the abdominal wall and the outline of the body in *Tuditanus walcotti* from the Coal Measures of Ohio. He has described, also, the fin membranes, the lateral line organs, the form of the body and the "pigmentum nigrum" of the eye of *Micrerpeton caudatum* from the Mazon Creek shales. Dollo has described an unusual amphibian from the Wealden of Bernissart, Belgium, *Hylæobatrachus croyii*, which showed the preservation of some of the body membranes and thus a portion of the form of the body. Numerous observers have written on the form of the feet in amphibia as they have been recorded by their footprints in the rocks.

Nothing has ever been contributed to the structure of the intestinal tract of the fossil amphibia, and from the nature of the case as well as from the extreme rarity of approximately complete specimens of these animals it would be an unexpected event if such were discovered. Our confidence in the preserving powers of the rocks grows, however, from year to year, and if we look long enough we can not fail to uncover many things of interest.

The amphibia of the Mazon Creek shales have always been noted for the unusual perfection of their preservation, which they have shared with other animals and with the plants from that historic locality. *Amphibamus grandiceps*, the first amphibian described from these shales, was made known in 1865 by Professor Cope from an almost perfect specimen. The next species made known from these shales was the form described in 1909 by the writer under the name *Micrerpeton caudatum*. It was based on a specimen which lacked only portions of the limbs of being complete. Nothing of the intestinal tract was observed in either of these species. It was somewhat surprising, on that account, to observe among a lot of specimens loaned the writer for study by Yale Museum, on two excellently preserved examples of the Branchiosauria, apparently adult, molds and impressions of what appeared at first sight to be intestines. Further study showed that in the smaller specimen there was preserved the *entire* alimentary canal and the other specimen had the alimentary tract approximately complete. There are no traces of branchiæ to be observed in either specimen.

The species which these forms represent is unknown and the writer has accordingly proposed for them, in another place, the name *Eumicrerpeton parvum,* new genus and species, and has regarded them as representatives of the family Branchiosauridæ. The smaller specimen has the more completely preserved canal of the two and the description given below will apply mainly to that specimen.

The nodule which contains this interesting little fossil measures two and a quarter inches by two inches and the fossil salamander occurs as nearly as possible in the center of the nodule (Fig. 4). The white kaolin which has usually replaced the bones in the Mazon Creek fossils has nearly all become eroded, only that of the right humerus remaining. The animal is of course preserved on its back.

If it were not for the fact that the œsophagus became loosened and dropped down from its place shortly after death, the alimentary canal would be in place and would immediately recall a freshly dissected specimen of a recent salamander. The anterior end of the œsophagus lies obliquely across the chest region with its tip pointing slightly downward. The length of the œsophagus proper is only about three millimeters. The entire animal measures but thirty millimeters in full length from the snout to the tip of the tail, the form of which is clearly preserved (Fig. 1).

The œsophagus, as it is preserved, lies in a semi-sigmoid curve with the convexity anterior. It enters the cardiac portion of the stomach by a gradual constriction. The stomach is clearly preserved as a distinct sac-like organ with two lobes which correspond to the cardiac and pyloric limbs. The stomach measures about seven millimeters in length by two millimeters in its greatest diameter. The muscular constriction which divides the organ into pyloric and cardiac divisions occurs at a distance of four millimeters from the upper end. The pyloris is designated by a rather pronounced constriction which may be partly accidental although it recalls the pyloris of the frogs very strongly. From this constriction, which lies on the left side of the fossil, as it is preserved, the duodenal portion of the intestine makes a straight course posteriorly to near the anal region, where it takes a sharp bend and curves back to run parallel with itself for the

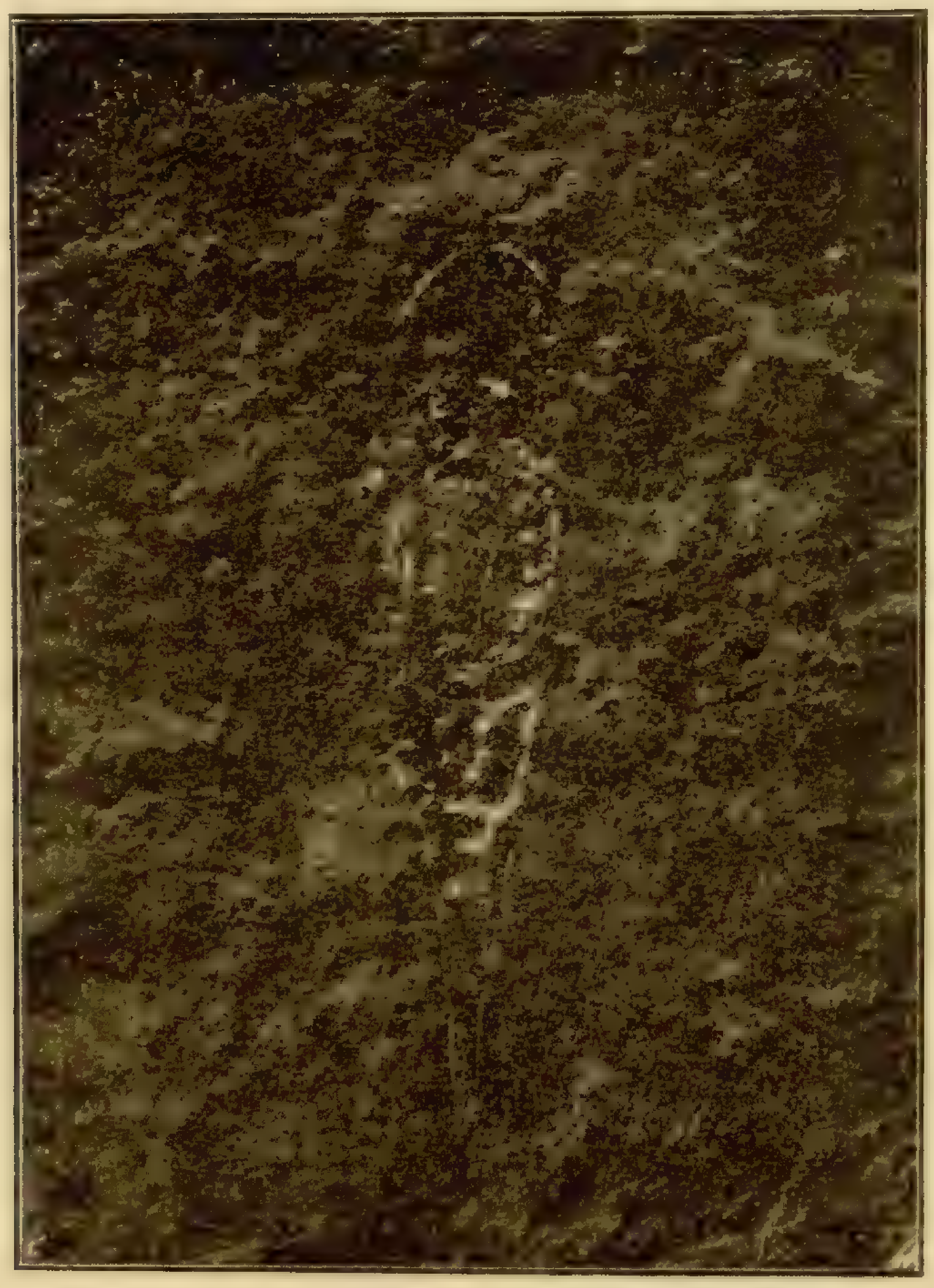


FIG. 1. An enlarged photograph of the smaller specimen of *Eumicrerpeton parvum* showing nearly the complete course of the intestine. × 2.

distance of four millimeters. In its upward course, immediately on leaving the anal region, the intestine enlarges and practically the same enlargement continues throughout the remainder of its course to the anus. At the distance of a millimeter from the anal end the rectum dilates probably an eighth of a millimeter to form the cloaca. After the intestine has continued its parallel course for the four millimeters as stated above, it turns abruptly to the right for a distance of two millimeters. It then runs posteriorly for a short distance, then bends back and under itself to again make a double sigmoid curve, when at a distance of six millimeters from the anus it assumes a straight course which it continues to the end (Fig. 3).

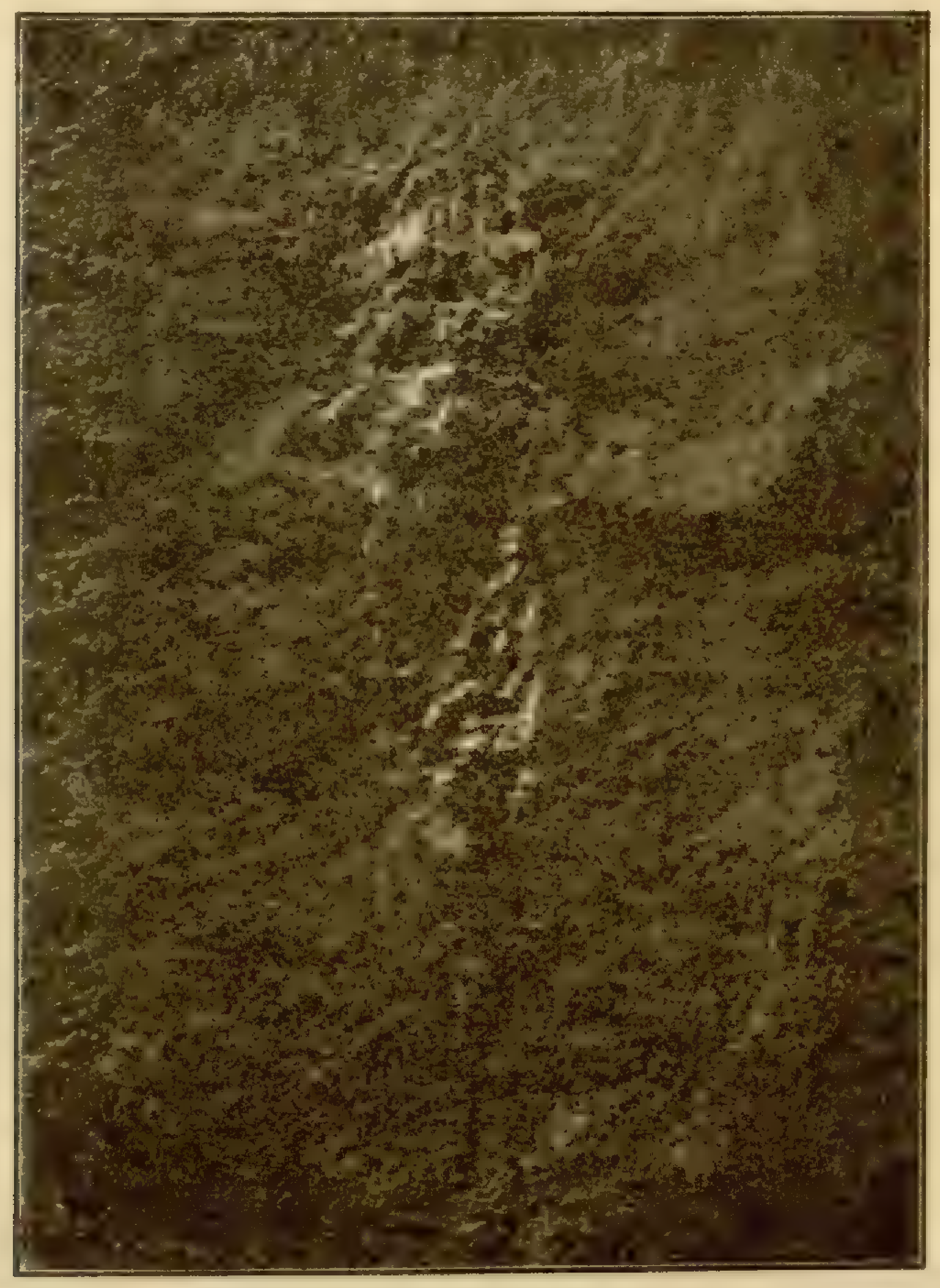


FIG. 2. An enlarged photograph of the larger specimen of *Eumicrerpeton parvum* showing portions of the impressions of the alimentary canal. × 2.

The anus lies at a level which is approximately that of the lower end of the femur, which is preserved as an impression on the left side of the fossil, thus agreeing in its position with that found in the modern Caudata. Lying inside of the curve of the stomach and partly inclosed by the œsophagus is a smooth area which may possibly represent the impression of some of the accessory digestive glands such as the liver. Occurring in this smooth area are numerous fine lines which possibly represent blood vessels; but they are so imperfectly preserved that I will not be sure.

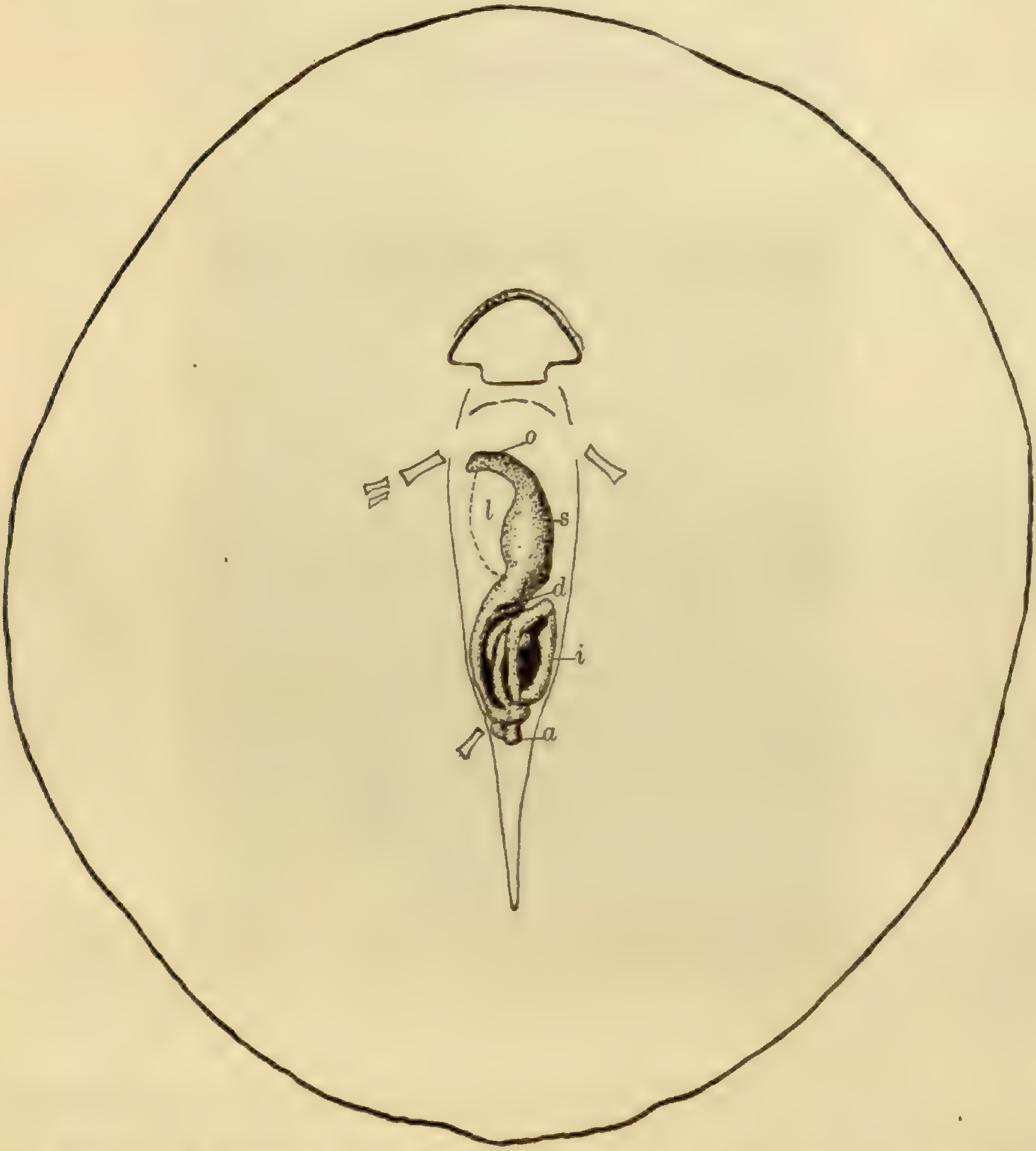


Fig. 3. A drawing of the smaller specimen of *Eumicrerpeton parvum* showing the full course and condition of the intestinal tract. × 2. *o*, œsophagus; *l*, liver; *s*, stomach; *d*, pyloris; *i*, small intestine; *a*, anus. Portions of the limb bones are also outlined as well as the anterior end of the interclavicle.

The other and larger specimen (Fig. 2) is some ten millimeters longer than the example described above. The alimentary canal is represented not as a mold, as in the specimen described above, but by an impression from which the mold has been lost. By taking a wax impression of this specimen the form of the œsophagus, stomach and portions of the intestines, with the same form and arrangement as has been described, are beautifully shown. The œsophagus has also in this specimen been loosened and dropped down. The anus is quite prominent and lies somewhat beyond the base of the tail. The tail is preserved entire in an elongate V. On its membranes are to be seen very clearly preserved the median and dorsal lateral lines which have been so completely described for *Micrerpeton caudatum*. Lying beside the anus in both specimens is a small elevation which may in both cases be accidental or it may represent either the posterior end of an oviduct or some anal gland which the branchiosaurians possessed.

FIG. 4. The nodule containing the smaller fossil shown natural size.

The modern amphibia present many problems for consideration. Among the most interesting of these is the one which is concerned with the phylogeny of the living forms. An attempt has previously been made by the writer[1] to elucidate the problem of descent so far as the Caudata are concerned. The present contribution is a further extension of that effort and it supports the conclusions there drawn.

Representatives of several genera of the modern Caudata have been dissected in order to make a direct comparison of the fossil alimentary canal with that of the recent forms. Among the forms dissected may be mentioned *Ambystoma tigrinum, Ambystoma opacum, Diemyctylus torosus, Diemyctylus viridescens, Desmognathus fuscus* Raf., *Spelerpes bilineatus* Green, etc. In some cases representatives of several stages in the growth of the individual species have been available for study. The alimentary tract of *Desmognathus fuscus* Raf. from the vicinity of Ithaca, New York, resembles in a marked degree that of the fossil form. The nearest approach to the condition there represented is, however, found in an immature branchiate individual of some 47 millimeters in length, of *Diemyctylus torosus* Esch., from a fresh-water pond on Orcas Island in Puget Sound. The presence of this species on the island is very suggestive and its bearing on the geological age of the caudate amphibia will be given elsewhere. It is of extreme interest that the condition represented by the fossil should resemble so closely that of an immature rather than a mature form since it lends support to the recapitulation theory. Perhaps the representative species of the genera *Desmognathus, Spelerpes, Hemidactylus,* etc., are forms which have become restricted in their development and thus represent more nearly in the structure of their alimentary canal the ancestral condition, as is also the case in the immature form of the *Diemyctylus torosus* Esch.

The writer has attempted to show that the modern

---

[1] AMERICAN NATURALIST, XLII, No. 498, June, 1908.

Caudata are forms which have evolved by a process of degenerative evolution and he has supported his contention by a direct comparison of the skeletal anatomy of the Branchiosauria and the Caudata. So far as the skeleton is concerned the caudate organization is less high than that of the Branchiosauria. Such can not be said of the alimentary canal, for it at least has progressed in its development in many forms, although, as has been stated above, some of the more slender species are apparently restricted in their development. The fact that a young form of *Diemyctylus torosus* shows a closer approach to the fossil condition than any other is of extreme interest. It can be said with certainty that the *Diemyctylus torosus* goes through the phylogenetic stages in the development of its alimentary canal and in my opinion we have here a representative in the fossil condition of one of these phylogenetic stages. But too much importance can easily be attached to the close resemblances outlined above. It is to be remembered in this connection that the form of the alimentary canal is so highly modified by the food habits and by the form of the body of the individual animal that it will be difficult to draw safe conclusions. On the other hand, so far as we have ascertained, the form of the body of the salamanders has not changed essentially from that of their forebears, the Branchiosauria, so there is no really good reason why the form of the alimentary canal should have undergone much change.

SHORTER ARTICLES AND CORRESPONDENCE

OBSERVATIONS ON THE SPAWNING HABITS OF HYDROIDES DIANTHUS

In connection with experiments and observations on the behavior of several species of annelids, chiefly the one above named, covering a period of several years, it was my good fortune to have seen the apparently somewhat rare phenomenon of the spawning of these annelids under circumstances peculiarly favorable for observation. So far as I am aware this has not been made a matter of record, at least for this species, and some inquiry among students of the group has failed to elicit any detailed knowledge concerning the subject. It seems to be worth while to submit my notes made at the time for at least a record of fact, trusting that they may prove interesting to that extent.

The observations were made upon specimens in an aquarium in my room at the Fisheries laboratory, Woods Hole, on July 30, 1908. A large colony, or aggregate, of these annelids had been freshly obtained from near New Bedford, and had been transferred to my aquarium about two hours before the spawning took place. This was soon after noon of the date mentioned and the first appearance of the discharge took place about two o'clock. I was sitting quietly by the aquarium observing the various aspects and attitudes of the specimens, when a single individual was seen to discharge suddenly a jet of whitish matter, which seemed like a milky spume. It was so unusual as to attract immediate attention, and within a few seconds the same specimen repeated the process. Almost immediately a second specimen made a similar discharge, ejecting a cloudy mass in a jet which extended from twenty to thirty millimeters from the worm, which at the time was extended perhaps about half that distance beyond the orifice of the tube. Almost immediately another specimen exploded in similar fashion, and in less time than it requires to make the record there were dozens actively discharging clouds of eggs and sperms, until the entire mass of water (at least six gallons), was milky with the generative products. The eggs soon settled downward, indeed at the time of ejection they were easily distinguishable, being ejected to a less distance and rapidly inclining toward the bottom. The spermatozoa, on the other hand, remained floating for an hour or more after the discharge had ceased. The operation went on for a period of some thirty or forty minutes, and then ceased almost as suddenly as it had begun. Within an hour or so the water had cleared of its milky aspect, the cells having settled to the bottom of the tank.

The phenomenon was unlike anything which I had ever seen among annelids. A single specimen would discharge at brief intervals in jets like puffs of steam from an engine, and at the height of the performance, when at least fifty specimens were thus engaged, it was a spectacle of the most striking and exciting character. If one could imagine some Lilliputian fire brigade of similar numbers all intent on discharging intermittent streams upon a miniature conflagration the impression could hardly be more engaging!

Antecedent Behavior.—It had been observed at the time of the transfer of the specimens referred to above, that there were quite a number of large specimens which did not retract fully into the tubes, as is usually the case under such an operation. This aspect was more or less persistent during the operation of handling, and if a specimen were compelled to fully retract by touching it with the finger it would soon reappear and protrude the anterior portion of the body. This protrusion was likely to continue even after they had been put quietly into the aquarium. It was this peculiarity which was engaging my attention at the time the sexual explosions began. The query arose as to whether it might not have been induced by some stimulus associated with the process of transfer and consequent exposure to extraneous conditions. Accordingly I took occasion to subject the colony to similar handling on subsequent days in order to assure myself concerning the matter. But in no case was it possible to induce a second discharge, or any simulation of the sort. It seems highly probable, therefore, that the phenomenon was perfectly normal, notwithstanding its apparently unusual character. During the several years in which I had similar colonies under observation in the same room for long periods it would seem as if *some* symptom of the sort might have been noted. In a letter from Professor J. Percy Moore I am assured that

Although I have kept large numbers of *Hydroides* literally bursting with genital products under observation, I have seen natural oviposition only twice.

Professor A. L. Treadwell has also stated that he has observed a similar operation in the egg-laying of *Dopatra*. He says further:

> Whether the epidemic of egg-laying, in which when one starts the others follow, is due to a similar stimulus acting on all of them at once, or whether the first one stimulates the others, is not certain. I should consider the latter the more probable explanation. I found that to be the case in *Podarke,* where, if one started, the whole dish was apt to explode.

So far as could be ascertained under casual observation the individuals participating in the performance were about equally males and females, a further indication of the essentially normal character of the phenomenon. It would seem as if specimens of approximately similar age and condition of maturity ripen the genital products at a given time, and under the appropriate stimulus discharge them simultaneously.

The behavior will recall the somewhat similar exhibition of the pololo worm, whose swarming and coincident spawning has been described by several observers. May we not conclude that these several phenomena are but varying expressions of a spawning habit more or less common in annelids, and indeed not unknown among other of the lower invertebrates, though differing of course in various details?

It may be mentioned in conclusion that the ova discharged by the worms at the time described were promptly fertilized and developed in a perfectly normal and regular fashion.

CHAS. W. HARGITT.

SYRACUSE UNIVERSITY,
January 14, 1910.

NOTES AND LITERATURE

PROTOZOA

Doflein's "Lehrbuch der Protozoenkunde."[1]—No group of animals affords a more direct approach to the problems of evolution than the Protozoa and few offer such varied data for their discussion. The organism and the individual are here reduced to lowest terms and the processes of growth, differentiation, degeneration, regeneration and reproduction in the most varied forms are found in astonishing variety and complexity. The phenomena of overcrowding, rapid destruction, parasites and parasitism, immunity, variation, speciation, isolation and perhaps even mutation, with all of their consequences on structure and reproduction, are illustrated in varying degrees of diversity and completeness. It is therefore to be expected that a thoroughgoing review of the rapidly augmented literature of protozoology by Professor Doflein will yield some new points of view or at least a new perspective in which old conclusions and hypotheses may be tested.

The biogenetic law, for example, in the opinion of the author of the "Lehrbuch" is very doubtfully applicable to the Protozoa. External factors profoundly affect the form and structure of these simple organisms. Increased alkalinity of the water changes *Amœba limax* to *A. radiosa,* as Verworn has shown. Trypanosomes vary greatly in appearance and virulence, according to the hosts in which they are cultivated, and in culture media locomotor organs are lost and nucleus and blepharoplast are shifted into new relations in the cytoplasm. Reproductive processes are profoundly modified by temperature and chemical media. The kind of food, according to Faure-Fremiet, affects the structure of *Vorticella.* The form changes, therefore, through which a protozoan runs in its life cycle are to be regarded as moulded by external influence rather than by internal factors of heredity and the production of similar structures is a phenomenon of convergence rather than a proof of relationship or descent.

This point of view determines Doflein's treatment of certain important questions. Thus the Suctoria form a class coordinate with the Ciliata since the posterior circlet of cilia formed on the bud of *Acineta* is a convergence phenomenon attendant upon the free-swimming life of this stage rather than primarily an ancestral character indicating the derivation of the Suctoria from the Ciliata.

---

[1] "Lehrbuch der Protozoenkunde." Eine Darstellung der Naturgeschichte der Protozoen mit besonderer Berücksichtigung der parasitischen und pathogenen Formen. Zweite Auflage der "Protozoen als Parasiten und Krankheitserreger." Von Dr. F. Doflein. Pp. x + 914. Mit 825 Abbildungen im Text. Jena, Gustav Fischer, 1909. M. 24. Geb. 26.50.

Again the occurrence of flagellate-like stages in the life history of the *Plasmodium, Babesia* and *Leishmania* is not regarded as of phylogenetic significance but as an independently derived adaptive stage. The Hæmosporidia are therefore not transferred from the Sporozoa to the Flagellata by Doflein as Hartmann and others have argued. On the other hand, the trypanosomes are regarded as having been derived from parasites of insects such as *Herpetomonas* and *Crithidia*, whose forms they resemble in culture media.

Doflein is skeptical about the specific distinctness of the various pathogenic trypanosomes of mammals, though recognizing the necessity of distinguishing them to avoid confusion, by their hosts, occurrence and typical form in the blood of the host. They are forms merely, not fixed species, and doubtfully even incipient species. He holds as uncertain even the specific distinctions in the so-called gametes of *T. gambiense* and *T. brucei* in the tsetse fly reported by Koch. He also rejects as hypothetical the sexual cycle of *T. lewisi* in the rat louse reported by Prowazek, regarding the evidence as based on abnormal stages altogether too rare in occurrence to be typical sexual phases. However the more recent work of Minchin, Baldry and Breinl and Hindle tends to confirm the view that a sexual phase of the parasite may occur in the insect host.

The Protozoa are regarded as a group whose limits are arbitrarily defined in the interests of economy in scientific work rather than by structure. No sharp boundary line separates then on the one hand, from the Metazoa—witness the spore of *Nosema* or that of the *Actinomyxidia*—or, on the other, from the lower Metaphyta, as may be seen in the family Volvocidæ within which numerous types of colonial organization have been evolved. Not only do the Protozoa intergrade with Metazoa, the lower algæ, moulds and fungi in morphological characters, but also in physiological as well.

The author has for some years consistently maintained that the lowest branch of the Protozoa is not the Rhizopoda as stated in practically all text-books and manuals, but rather that the Mastigophora are to be regarded as lowest in the scale of organization. This is based not only upon the occurrence of flagellated forms in the gametes or other reproductive phases in the life history of other classes, but also upon the relationships of the Mastigophora to the Bacteria. This relationship is traced by Doflein through the Spirochætes which he names also Proflagellata, to *Spirillum* and like forms. The suggestion is made that the Bacteria are the equivalents of postulated Monera of Haeckel, though they are far from resembling the forms actually described by him as Monera, and that bacteria other than *Spirillum* should be in like manner attached to other groups of protists to which they may be related. Attention is called to the wide-spread occurrence among Protists of chromidial cells, that is those seemingly without nucleus but having finely divided and distributed chromatin as seen in Bacteria, *Oscillaria, Nostoc* and *Tetramitus* and to the appearance of this same type of distribution of chromatin throughout the cell body among Protozoa at certain stages of life history, especially in gametogenesis, though also in hunger-stages and in pathological conditions. He wisely sounds a note of warning against the domination in protozoology of the morphological conception based upon the Metazoan cell, and a note of caution against the possible interpretation of minute parasites as chromidia. Ingested chromatin, as Martin has shown in the Suctoria, also offers a pitfall for the chromidia hunter.

The theory of Schaudinn and Goldschmidt of the fundamental dualism of the nuclear substance in the Protozoa, of the existence side by side in the cell of sexual chromatin as exemplified in the micronucleus of *Paramecium*, of the generative chromidia of the Foraminifera, and the nuclear membrane substance of *Acanthometra* and of somatic chromatin as seen in the macronucleus of the ciliates, he regards as only a convenient morphological schema not justified by either the comparative morphology or the physiology of the Protozoa as a whole. He inclines rather to Hertwig's view of the unity of the chromatin substance.

Dr. Doflein acknowledges the great service which the theory of Hertwig regarding the proportions of nucleus and cytoplasm has rendered to science in the stimulation of research, but looks to the future to assess its permanent value. He suggests that depression stages resulting, on the one hand, in the regulating processes of sexual reproduction or, on the other, in degeneration and natural death, are exceptional "in der freien Natur." To the reviewer the astounding fluctuations[1] in numbers which the organisms of the fresh-water plankton undergo in short periods of time of three to five weeks, rising from minimum numbers to maximum of extreme proportions and falling away again with equal or greater abruptness with accompanying high death rate and appearance of sexual reproduction, especially in rotifers, seem to be of a similar nature to the cycles with intervening depression periods in laboratory cultures. These occur, moreover, constantly and with surprising regularity in nature, in both marine and fresh-water plankton among organisms of short life-cycles.

---

[1] Kofoid, C. A., 1908, "Plankton of the Illinois River," Pt. II, Constituent Organisms and their Seasonal Distribution, *Bull. Ill. State Lab. Nat. Hist.*, V. 8.

Certain points in both Schaudinn's and Hertwig's theories of sexual reproduction are combined with the earlier suggestions of Bütschli in a theory of sex which has much in common with that put forth by Geddes and Thomson. Living cells are conceived as consisting of two groups of substance, one more fluid in consistency concerned with the dynamic activities such as cell division and locomotion, the other more solid, the reserve stuff for the activities of life. In cell division these substances are not equally distributed, reserve stuff predominates in some (females) and the locomotor substance in others (males). Morphological cell constituents for these substances are expressly not postulated. An indifferent protozoan by division gives rise to equal numbers of differentiated male and female individuals, whose differentiation increases as division progresses. Fertilization takes place in consequence of the physico-chemical attraction of the two substances. The same chemical differences which condition the form-distinctions of the gametes are also the prime cause of the union in fertilization.

This theory naturally is easily applicable to the indifferent, male and female forms of Trypanosomes and to the highly differentiated sexual process and gametes of the Sporozoa generally, but requires further elucidation to make it applicable to isogamy, which is perhaps the primitive type of sexual reproduction and one seemingly widespread among Protozoa.

Dr. Doflein's book is not only a great mine of carefully and critically assembled information on Protozoa, but his facts are marshaled with reference to the great problems underlying all biological work in such a way as to stimulate further research.

Charles A. Kofoid.

University of California.

CELEBRATING DARWIN'S GREATNESS AND DARWINISM'S WEAKNESS

It will seem less ungracious now that the year has turned, the one-hundredth year since Darwin's birth and the fiftieth since the "Origin of Species," to say that the many memorial meetings of the past year have left the definite impression on the scientific world of having celebrated Darwin's greatness and Darwinism's weakness. This is particularly true of the most important and conspicuous two of these meetings of which the books[1] under my eye at this moment are the permanent published record.

The eleven addresses of the "Fifty Years of Darwinism" volume are, with one exception, by American naturalists. And, with that same exception, and perhaps one other, all sound clearly the note, now more pronounced, now more restrained, of positive adverse criticism of the Darwinian factors in evolution. Each speaker first recognizes the lasting debt of science and of himself to the immortal master, and then gently or forcefully proceeds to show how the master's explanation fails to explain, and to unload and display his own precious personal baggage of "factors": factors of environment, of mutation, of adaptation, of determinate variation, of isolation and what not.

It is, of course, greatly gratifying to us all, in these very times of loud bewailing of the insufficiency both in quantity and in quality of American output in research and natural-philosophic thought, that each of the distinguished speakers at the chief American Darwin memorial meeting had his own personal baggage of evolution contributions to unload. In a pinch we can make, by discriminating concentration, a very creditable showing for American activity in the biological "higher thought." "Fifty Years of Darwinism" certainly proves this.

The exception to the chorus of criticism and contributions to substitute for the selection theories, or, at any rate, to come to their imperatively needed aid because of some partial but fatal weakness, is embodied in the address of the one English participant in the meeting. Professor Poulton, with a glorious patriotism that surpasses that of the defender of imperialism, of an hereditary legislative body or a staggering naval budget, defends all of Darwinism against all of its critics.

For the rest, the names of Chamberlain, Coulter, Jordan, Wilson, MacDougal, Castle, Davenport, Eigenmann, Osborn and Hall show the scope and authority and interest of these addresses.

At the great English meeting there were more than twice as many essayists and the book that publishes them is twice as large as the American book. Of the twenty-nine speakers eighteen were British and eleven foreign (two American, six German, one French, one Danish and one Dutch). Also the subject covered was much broader than that of species-forming, heredity and adaptation. It ranges from embryology to the genesis of double stars; from the structure of the cell to the bases of religious faith; from the movements of plants to the evolution of matter. The greatest Neo-Darwinian and one of the greatest Neo-Lamarckians were there; as were the most radical mechanicalist, the most advanced monist, the most ardent Mendelian, the founder of the mutations theory, one of the most influential of modern philosophers, and the four distinguished sons of the immortal master. It was a more representative gathering than the American one if for no other reason—though there are other reasons—than that twenty-nine men are likely to be more representative than eleven, or that six nationalities are likely to represent more than two.

---

[1] "Fifty Years of Darwinism," Eleven Centennial Addresses in Honor of Charles Darwin, 1909, H. Holt & Co., New York, $2.00.

"Darwin and Modern Science," Essays in Commemoration of the Centenary of the Birth of Charles Darwin and of the Fiftieth Anniversary of the Publication of "The Origin of Species," 1909, University Press, Cambridge, and G. P. Putnam's Sons, New York, $5.00.

But the points in common to both meetings were exactly those indicated by the title of this review. And these are the points common to almost all present-day critical discussion of evolution and its explanations. Darwin's explanations are no longer sufficient; they never were, of course, but they seemed so. But Darwin himself as man and worker, as example, as real establisher and greatest champion of the whole organic evolution conception, shines ever more brilliantly in the heavens of history.

De Vries, Weismann, Bateson, Haeckel, Lloyd Morgan, Goebel, Klebs, Sedgwick, W. B. and D. H. Scott, Loeb, Schwalbe, Arthur Thomson, Strassburger, Joseph Hooker, Thiselton-Dyer, Gadow, Francis and George Darwin, Poulton, and the nine others that represented geology, physics, philology, history, sociology, philosophy and religion, make up an imposing list of names in modern biological science. It is the list of the essayists at the Cambridge meeting. Add to it the names, already catalogued, of the participants in the American meeting, and the possessor of the two books that contain these many addresses and essays may confidently assume himself to be in possession of the latest authoritative word in evolutionary matters.

V. L. K.

Stanford University,
February, 1910.

BOOKS **WILLIAM J. GERHARD,**

2209 CALLOWHILL STREET, PHILADELPHIA, PA.,

offers the following at affixed net prices. Extended catalogues of books and pamphlets in all branches of natural history post-free on request :

1.	American Journal of Conchology. 7 vols., partly bound	$25.00
2.	American Journal of Science. Second Series, volumes 1–10. Half roan (3 vols. somewhat waterstained)	10.00
3.	American Mineralogical Journal (Bruce). 1 vol., 1814. New half morocco	10.00
4.	American Monthly Microscopical Journal, vols. 1–20 (1888–1899), of which 14 vols. are half roan	15.00
5.	American Naturalist, vols. 1–6 (1868–72)	9.00
6.	Annals N. Y. Academy of Science, vols. 4–14 (1887–1898). Cloth	22.50
7.	Annuaire du Musée Zoologique de l' Académie des Sciences, St. Petersbourg, vols. 1–7 (1896–1902), lacking one number of vol. 1	10.00
8.	Bulletin American Museum of Natural History, vols. 1–11 (1887–1901)	27.50
9.	De Kay. Zoology of New York—Birds. 4to. Cloth. 141 colored plates	10.00
10.	Gaudry, A. Animaux fossiles et géologie de l'Attique. 2 vols., folio, 1862–67. Half calf, 75 plates and map	35.00
11.	Harlan, R. Medical and physical researches, etc. 1835. Cloth	7.50
12.	Journal and Proceedings Royal Society of New South Wales, vols. 11 (1877) to 23 (1890), except vol. 14. Partly bound in cloth	13.00
13.	King, C. United States Geological Exploration of 40th Parallel. Complete set, 7 vols., quarto, cloth, and two folio atlases	22.50
14.	Microscope (The), vols. 4–11. 8 vols. in four. Half roan	7.50
15.	Morton, S. G. Synopsis of the organic remains of the cretaceous group of the United States. 1834. Half roan. Rare	15.00
16.	Pritchard, A. History of Infusoria, including Désmidiaceae and Diatomaceae. Fourth (last) edition. 1861. Half morocco	8.00
17.	Proceedings Lit. and Philos. Society of Liverpool, vols. 1–34 (except vols. 5, 10, 11, 12, 16, 17, 20, 21), partly bound	16.00
18.	Reports of Explorations and Surveys . . . for a railroad from Miss. River to Pacific Ocean. 13 vols. 4to. Bound	12.00
19.	Smithsonian Miscellaneous Collections, vols. 1–6 (1861–67). Scarce	13.50
20.	Sowerly and Lear. Tortoises, terrapins and turtles drawn from life. Small folio, 1872. Half morocco, 60 finely colored plates	11.00
21.	Transactions American Entomological Society, vols. 1–6. Bound. Scarce	35.00
22.	Transactions Geological Society of Pennsylvania. 1 vol. (1835.) All issued. New half morocco. Rare	15.00
23.	Winter, G. Die Pilze Deutschlands, etc., vols. 1 and 2 (1884–87). Half morocco	7.50

Methods in Plant Histology

By CHARLES J. CHAMBERLAIN

Second edition, revised and much enlarged; 272 pages, with 88 illustrations, 8vo, cloth; net $2.25, postpaid $2.39

THE first complete manual to be published on the subject of botanical microtechnique. It contains detailed directions for collecting and preparing plant material for microscopic investigation, setting forth the advantages and disadvantages of the different methods.

Will no doubt find a place in every well-regulated library, and will be found very useful by private students.—*Plant World.*

It is an excellent book for the individual worker and for classes in colleges.—*Education.*

A Laboratory Guide in Bacteriology

By PAUL G. HEINEMANN

158 pages, interleaved, with 37 illustrations, 12mo, cloth; net $1.50, postpaid $1.61

A CLEAR and concise presentation of bacteriological technique, designed principally as a manual for the medical student, but highly useful also as a reference book for the biological teacher and investigator, as well as for practical workers in the fields of medicine and hygiene.

The instruction given is clear and accurate, and the practical exercises are well selected.—*The Lancet* (London).

A book such as this must facilitate very greatly the practical class work, for which it is most excellently adapted. — *American Journal of Medical Sciences.*

The directions are clear and concise, and every stage is described so carefully that it is hard to see how the student can go astray. Physicians who are rusty in bacteriology cannot do better than buy this little book. The book is beautifully printed and bound.—*American Journal of Clinical Medicine.*

Animal Micrology:

Practical Exercises in Microscopical Methods

By MICHAEL F. GUYER

250 pages, 8vo, cloth; net $1.75, postpaid $1.88

THE title of this book will explain its scope. It is intended as a laboratory manual for textbook use. Its aim is to introduce the student to the technique of microscopic anatomy and embryology, emphasizing details of procedure rather than descriptions of reagents or apparatus. Sufficient account of the theoretical side of microscopy is given to enable the student to get satisfactory results from his microscope.

The directions are simple, explicit, and complete.—*American Journal of Clinical Medicine.*

The medical student will find it very useful as a guide to microscopic work.—*Journal of the American Medical Association.*

This is one of the cleanest works on microscopical technique we have ever seen, and is especially suitable for the beginner. It is full of points, tricks of technique not mentioned in other works, and is one that every student and physician should have.—*Medical Century.*

This valuable book is strong through its rigid exclusion of the trite and the conflicting. It is lucid and helpful, because a man long practiced in practical work has given what he believes the most expeditious and reliable method of obtaining a definite and comprehensive result. — *Medical Notes and Queries.*

A concise, eminently practical, and well-classified treatment.—*Science.*

The expositions of the methods recommended are admirably clear.—*Nature.*

One of the best and most practical works upon microscopic technique with which we are acquainted.—*American Naturalist.*

As a textbook it can hardly be improved. The research worker will find in this book just the information he frequently needs in preparing material with which he is not familiar.—*School Review.*

It does present in very clear form a judicious selection of methods, including an excellent untechnical account of the microscope and its optical principles, adequate for the undergraduate course in histology.— *Journal of Comparative Neurology and Psychology.*

ADDRESS DEPT. 64

Chicago **THE UNIVERSITY OF CHICAGO PRESS** **New York**

VOL. XLIV, NO. 523 JULY, 1910

THE
AMERICAN
NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with
Special Reference to the Factors of Evolution

CONTENTS

Page

I. A Consideration of the "Species Plantarum" of Linnaeus as a Basis for the Starting Point of the Nomenclature of Cryptogams. Professor W. G. FARLOW - 385

II. Notes on Some Beaufort Fishes. E. W. Gudger - 395

III. On the Effect of External Conditions on the Reproduction of Daphnia. Dr. J. F. McCLENDON - 404

IV. Are Fluctuations Inherited? Dr. HARRY H. LOVE - 412

V. Inheritance in Potatoes. Professor EDWARD M. EAST - 424

VI. Shorter Articles and Correspondence: The Age of Speed Sires: Professor F. R. MARSHALL - 431

VII. Notes and Literature: Russo on Sex-Determination and Artificial Modification of the Mendelian Ratios, Professor W. E. CASTLE; The Bubonic Plague, Professor H. B. WARD; Desert Plants, Professor WILLIAM L. BRAY - 434

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

TO ORNITHOLOGISTS AND MUSEUMS

W. F. H. ROSENBERG

Importer of Exotic Zoological Specimens

57 Haverstock Hill, N.W., England

Begs to announce the publication of a new Price List (No. 11) of **Bird Skins.** This catalogue contains over 5,000 species, and is the largest and most complete price list of birds ever published. It is arranged in systematic order, based on the classification of the British Museum "Catalogue of Birds," with authors' names, indications of localities, and an index to families. It will be sent gratis and post free on application, as will the following lists:

No. 7, Mammals; No. 8, Birds' Eggs;
No. 9, Reptiles, Amphibia, and Fishes.

Largest stock in the world of specimens in all branches of Zoology.

Specimens sent on approval.

Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

Henry Holt & Company

34 West 33d St., New York
378 Wabash Ave., Chicago

Microscopes and Accessories

Hand Cameras of Highest Quality

Binoculars, Prism and Galilean

the best obtainable for Nature Study

Scientific Instruments

Laboratory Apparatus

Max Meyer 18 West 27th St. New York

"Quality, Prices, Service Right."

THE
AMERICAN NATURALIST

Vol. XLIV *July, 1910* No. 523

A CONSIDERATION OF THE "SPECIES PLANTARUM" OF LINNÆUS AS A BASIS FOR THE STARTING-POINT OF THE NOMENCLATURE OF CRYPTOGAMS[1]

PROFESSOR W. G. FARLOW

Harvard University

At the Congress held in Vienna in 1905 it was voted to adopt Linnæus's "Species Plantarum," 1753, as the starting-point of the nomenclature of flowering plants and the question of the starting-point for that of cryptogams was referred to the congress to be held at Brussels in May, 1910. The adoption of the "Species Plantarum" was endorsed practically by so large a proportion of phænogamic botanists that its acceptance came as near being universal as could ever be expected in such a case. It may be assumed therefore that the "Species Plantarum" is well adapted to serve as a basis for the nomenclature of phænogams. Were it true that it is as well, or nearly as well, adapted to serve as a basis for the nomenclature of cryptogams, there would be no hesitation on the part of cryptogamists in adopting it also. If it is not, there is no reason why they should feel under any obligation, for the sake of a merely formal uniformity in nomenclature, to follow in the steps of other botanists.

In the first place we may ask why it is that the "Species

---

[1] Invitation papers read at the sixteenth annual meeting of the Botanical Society of America.

Plantarum'' should be considered to be well adapted to the requirements of phænogamic botanists. The fact that it was the first work in which the binomial nomenclature was methodically applied is a sufficient reason why no work issued prior to 1753 should have been adopted as a basis of nomenclature, but that fact alone is not a sufficient reason for the adoption of the ''Species Plantarum'' itself. An examination of that work shows also other merits which should recommend it. It is an admirable summary by the leading systematist of his day of several hundred genera and some thousands of species found not only in Europe but also in North America and other more remote parts of the world. In fact, on glancing over its pages one is surprised at the large field covered by Linnæus and the large number of exotic species which are included in the work. In the numerous editions of the ''Species'' issued at intervals of a few years until as late as 1830, some under the title of ''Systema Vegetabilium'' and ''Systema Plantarum,'' the Linnæan traditions were handed down with additions and annotations by well-known botanists, so that there is no gap separating the original edition from the date of the appearance of the first volume of De Candolle's ''Prodromus'' in 1824. It should also be borne in mind that under the careful guardianship of the Linnæan Society of London, the Linnæan herbarium is still in existence and accessible to botanists. It is therefore not difficult to see that for a basis of nomenclature of flowering plants the ''Species Plantarum'' was well chosen.

If we turn now to the cryptogams of the ''Species'' we find a very different state of things. To those who have not examined the ''Species'' with reference to this point it might seem that the cryptogamists for the sake of uniformity might be willing to make some sacrifice. For such persons a comparative examination of the phænogams and cryptogams in the ''Species'' may be of interest. For this purpose I have prepared a table showing the number of genera and species in the two groups.

The number of genera can be determined without difficulty. The counting of the species is less easy since in some cases it is not quite certain whether under a given name Linnæus intended to indicate a species properly speaking or merely a form or variety. In my enumeration I have included only those forms clearly designated as species, omitting subspecific forms. That the enumeration here given is conservative is shown by the fact that, while according to the "Codex Linnæanus" the total number of species in the "Species Plantarum" is 5,938, the total of my list is 5,247, divided as follows:

	Genera.	Species.
Phænogams	1,049	4,630
Cryptogams	50	617
Total	1,099	5,247

Of the 50 genera and 617 species, 16 genera and 189 species are Filices and there are in addition 24 species of the genus *Lycopodium* which was placed by Linnæus in Musci. Among the Filices are to be found numerous characteristic species of America and the tropics and in this respect the treatment of the group by Linnæus is quite comparable with his treatment of phænogams. For nomenclatorial purposes the Filices and *Lycopodium* are even at the present day treated in the same manner as phænogams, and it is a well-known fact that it is the custom to unite the vascular cryptogams and the phænogams in floristic works. So far as we are now concerned the higher cryptogams need not enter into the discussion, but from the nomenclatorial standpoint must be classed with phænogams and there are therefore left 404 species and 44 genera for all the Bryophytes and Thallophytes described in the "Species Plantarum." But even in this small number is included the genus *Spongia* under Algæ with 11 species, of which at least the greater part are not even plants in any sense. Furthermore, among the Bryophytes and Thallophytes there are almost no extra-European species and of the European species a great proportion are northern. In short, although as far as phænogams are concerned the "Species Plantarum" includes characteristic representatives of different parts of the world, as far as the Bryophytes and Thallophytes are concerned it represents only a limited European flora.

The question may perhaps be asked by those who have not studied specially any group of non-vascular cryptogams: Although the number of non-vascular cryptogams in the "Species Plantarum" is very much smaller than that of phænogams, is it not perhaps the case that the ratio represents approximately the relative size of the two groups in nature? It has been the custom to state that the phænogams outnumber the cryptogams, some even saying that they are much more numerous. Such statements are based solely on an enumeration of described species and fail to give information as to the probable actual number of species. It is not possible to give figures on the subject which are up to date and the statistics of even a few years ago are of slight value, for it is only within a few years that the study of cryptogams has been pursued in other parts of the world than Europe or, to a less extent, North America. We can probably obtain a more correct opinion if we consider probabilities. The number of known species of Musci and Hepaticæ has been very much increased in the last few years, and although the bryological flora of Europe and North America is now so well known that no very large number of new species is to be expected there, in other parts of the world and especially in the tropics, it is evident that the work of exploration conducted by trained specialists will bring to light a very large number of new species. The same is true of lichens. In algæ a very great increase of species is less to be expected, partly for the reason that the region of growth of marine algæ, pelagic species excepted, is more limited than that of land plants. But even in algæ, it is probable that the known species will be considerably increased.

The fungi offer a better field for comparison than other groups. It is certainly true that the number of described species is decidedly smaller than that of phænogams. Are we then to conclude that there are fewer fungi in the world than there are phænogams? By no means, for there is a possible inference which may be drawn from a knowledge of the distribution of fungi to which, it seems to me, great weight should be given. Year by year the number of known parasitic fungi goes on increasing and, although we can not assume that probably every phænogam has its parasite, the proportion which have is constantly increasing. We also know that some species have not only one but many parasites and, as a rule, the species which from their economic value have been most carefully studied are the hosts of many fungi. As an instance I may mention the species of the genus *Vitis,* on which several hundred species of fungi are known to grow, some, to be sure, found also on other plants, but a large number peculiar to this genus. When all genera have been studied as carefully as *Vitis* we shall undoubtedly find that the number of parasitic fungi in existence is enormous. If to the parasitic we add the thousands of saprophytic fungi, it may well be asked whether eventually it will not prove to be true that the number of species of fungi is as great as that of phænogams. It seems to me that it should be plain to every one that if in the "Species Plantarum" the proportion of phænogams to cryptogams is about ten to one, we must admit that although the work is sufficiently comprehensive to serve as a basis for the nomenclature of the former, it is entirely inadequate in the case of the latter.

I have referred to the restricted range of the species of cryptogams described by Linnæus and to their small number. If we go farther and examine the character of the descriptions themselves we find that they are in many cases vague and unintelligible, which is nothing more than might have been expected in that day before the scientific study of the group had really begun. The Algæ in particular are from the modern point of view a strange medley. The genera *Jungermannia, Targionia, Marchantia, Blasia, Riccia* and *Anthoceros* I have in my enumeration included in Bryophytes where they properly belong, although they were placed by Linnæus in Algæ as well as the genus *Lichen* with 80 species. The genus *Tremella* with 7 species was also included in Algæ, although as far as the scanty descriptions can be identified, 3 are species of fungi, 3 algæ and one a lichen. Some of the 12 species of *Byssus* are algæ, but the majority it is impossible to recognize. Of the 11 species of *Spongia* nearly all are animals.

Of the later editions of the "Species Plantarum" the fourth, according to some the fifth, has a partial revision of the fungi by Link and of the mosses by Schwaegrichen, but as these parts were not published until 1824–30 and do not follow in any way the original edition of Linnæus, so far as priority of nomenclature is concerned, they need not be considered here. Of the "Systema Plantarum," Reichard, 1780, and the "Systema Vegetabilium" by Gmelin, 1796, by Persoon, 1797, and Sprengel, 1827, it can be said that although they include more species than the original edition of Linnæus they are open to the same objection and, as will be seen later, the dates of their publication are so near those of far better works that their nomenclatorial value is of trivial importance. If I have dwelt at what may seem too great length on a consideration of the value of the "Species Plantarum" as a basis of nomenclature, it has been for the purpose of trying to make clear to those to whom uniformity in nomenclature seems to be of the first importance, why it is that to expect cryptogamists to adopt the "Species" on the same basis as do phænogamists is unreasonable. To the latter the "Species" represents a fundamental treatise; to the former a very meager and unsatisfactory list of plants belonging to groups of which, in the time of Linnæus, there was really no exact knowledge.

One would be glad to adopt as a basis of nomenclature some one work which bears the same relation to cryptogams as does the "Species Plantarum" to phænogams, but there has never been any such work and there never will be, for a very good reason. The phænogams form a homogeneous group. The cryptogams do not, but consist of a number of different groups, and the fundamental works relating to them appeared at different dates, all, however, considerably later than 1753. The specialists who study bryophytes, lichens, algæ and fungi are entirely justified in adopting different works as a basis of nomenclature. The question they should ask is: What was the first work on bryophytes, on lichens, on algæ, on fungi, in which those groups were scientifically and comprehensively treated?

It is not possible to enter at this time on a general consideration of this point. Although that part of Linnæus's "Species" which relates to bryophytes appears to have greater value than that which relates to thallophytes, since for one reason his citations of Dillenius's figures help one to understand to what plants the brief descriptions were applied, it must certainly be admitted that Hedwig's "Species Muscorum," of which the first volume appeared in 1801, is the fundamental work on mosses and that Hedwig, with whom the scientific study of mosses began, may be called the Linnæus of bryology. Acharius stands in the same relation to lichenology, and it is a question to be settled by lichenologists whether the "Lichenographia Universalis" of 1810 or the earlier "Methodus" is to be given the preference. For algæ, the "Systema Algarum" of C. A. Agardh has been suggested. It is, however, out of the question to refer more in detail to the groups just mentioned, but it will be sufficient if we consider the case of fungi somewhat more minutely, although the subject is perplexing and complicated even to those more particularly interested in this group and probably wearisome to others.

In the "Species Plantarum" 1,073 pages are given to phænogams, 15 pages only are given to fungi, including *Agaricus* 27 species, *Boletus* 12, *Hydnum* 4, *Phallus* 2, *Clathrus* 3, *Elvela* 2, *Peziza* 8, *Clavaria* 8, *Lycoperdon* 9 and *Mucor* 11. To these must be added 3 of the species of *Tremella* placed by Linnæus in algæ, making 89 fungi in all. Of these not one is extra-European and only 8 are cited as growing in Italy or southern Europe. To consider that a work of such a limited scope should serve as a basis of nomenclature of a group whose species are numbered by thousands seems to me preposterous. All that we can say of the fungi in the "Species Plantarum" is that they show plainly that in 1753 next to nothing was known of that large group, and one may be pardoned for saying that in what Linnæus wrote about fungi he was not a Linnæus. We must search elsewhere for a fundamental work on the subject. In the later editions of the "Species" and the "Systema Vegetabilium," as I have said, the treatment of fungi is not in any way satisfactory, and it was not until about fifty years after the publication of the "Species" that there appeared anything which could be called a general and comprehensive work on the species of fungi. If mycologists were asked who exerted the greatest influence in placing systematic mycology on a firm basis they would say Elias Fries and the "Systema Mycologicum," of which the first volume appeared in 1821, had an influence in shaping the study as no other work has had. In saying this I do not wish in any way to underrate the value of the "Synopsis Methodica Fungorum" of Persoon, issued in 1801, but of the two I think that the "Systema" is the one which has had decidedly the greater influence in shaping the progress of descriptive mycology. In its three volumes together with the two volumes of the "Elenchus" which is a part of the "Systema," we find for the first time an account of the mycological flora of a considerable portion of the world rather than an account of certain orders of fungi, mainly of Europe. In the "Epicrisis" of 1836–38, the "Summer Vegetabilium Scandinaviæ," 1849, and the

"Hymenomycetes Europæi," 1874, we have important revisions and commentaries by Fries of his earlier work. The "Icones Selectæ Hymenomycetum" include 200 plates executed under his supervision of species which cannot well be studied by dried specimens alone. The herbarium of Fries is still at Upsala and the "Scleromyceti Leuciæ," a collection of 450 small parasitic species, is to be found in herbaria in Europe and this country and has been the subject of critical commentaries by several botanists. The fact that the volumes of the "Systema" did not appear in the same year does not appear to me to present a serious practical difficulty, as Volume I containing Hymenomycetes appeared in 1821 (except *Solenia, Cyphelia* and the Tremellineæ, in Vol. II, 1822), Volume II, section 1, with Discomycetes appeared in 1822, Volume II, section 2 (p. 275), with Gasteromycetes (Angiogasters) and Pyrenomycetes in 1823, Volume III, sectio prior with Gasteromycetes, Myxomycetes and Perisporiaceæ in 1829, and Vol. III, sectio posterior (p. 261), with Fungi Imperfecti in 1832.

The "Synopsis" of Persoon, although to be preferred to any previous work, is considerably less extensive in the number and range of the species given than the "Systema," the number in the latter being about two and a half times as great and, in general, the "Systema" presents a decidedly more modern way of treating the group. A fuller consideration of the comparative merits of the "Systema" is out of the question in this place as it would require more time than can be allowed and because the details are such that they could not be readily followed except by mycologists who have studied the question minutely. I have no right to encroach further on your patience and need only, in conclusion, repeat that the "Species Plantarum" is quite unfit to serve as a basis for the nomenclature of fungi, and that the "Systema" of Fries seems to me to be better adapted for the purpose than any other work. In any case, to go back earlier than the "Synopsis" of Persoon would only tend to perpetuate the present uncertainty and confusion, and would open the door to those who, regarding nomenclature as an end in itself and not merely a means by which the necessary evil of naming plants can be reduced to a minimum, devote time and labor to the undesirable task of unearthing names which are at the best uncertain, at the sacrifice of names which have been in universal use for many years, and whose meaning is perfectly clear. To my mind the object should be, not to attempt to seek perfection in authority and priority—a hopeless task—but rather to select the best solid basis in some comprehensive work. Even then, there is the question of *genera conservanda* and I believe that, whatever work or date is adopted, it will be most desirable to adopt a list of *genera conservanda*. There is nothing illogical in this and practically there are great advantages unless one believes in the theory that mere changing of names is a merit in science. That theory I certainly do not accept, but hold that the fewer changes of names the better.

It has been my misfortune never to have found anything perfect. Some of my friends have perfect systems of classifications of books, of herbaria or of plants. In trying to apply perfect methods I always recall a visit in company with Sir Joseph Hooker to an establishment not a thousand miles from here. The person in charge said, "We think we have a perfect museum case which we would like to show you." "Yes," said Sir Joseph, "I am always glad to see what I have never seen. But what do you keep in the case?" A key was produced, but by no amount of coaxing or forcing could the case be opened. "Yes," said Hooker, "I presume that it is perfect, but I prefer cases which open." The same remark would apply to a good many systems. They are perfect until we try to find out what is in them.

NOTES ON SOME BEAUFORT FISHES—1909[1]

E. W. GUDGER

State Normal College, Greensboro, N. C.

The following observations were made while working at the Station of the Bureau of Fisheries at Beaufort, N. C., from May 26 to July 6, 1909, and are recorded in brief in the card catalogue of fishes in the laboratory. While they are but *membrana disjecta,* they are published in the hope that they may not be devoid of value to those interested in fishes.

These fishes, with the exception of the ones specifically noted from other localities, were taken at the Narrows of Newport River. This is a small stream, whose sunken lower valley is an estuary opening into and forming a part of Beaufort Harbor. The Narrows, distant some seven miles in a northeasterly direction from the laboratory, are at the head of the estuary. Here are a number of "rocks" or reefs built by oysters out on the mudflats. Their names, as one comes to them in going up stream, are Lawton's, Cross and Rockfish Rocks, and a fourth one not named. These reefs, extending out at nearly right angles from the shore, give the channel a very tortuous course. Above them the mudflats spread out so shallow that the river is not navigable save for small boats and by them only at high water. The waters of the ebb tides, collected off these mudflats and largely confined by the reefs to this narrow channel, surge around these points and have scoured out deep holes. Here are to be found large numbers of various fishes, which go up the river to feed on the mudflats and at low tide drop down into these holes. There is no seining ground at Beaufort, known to the writer, where so many different species of fishes may be taken at a single haul of the seine as at the "Rocks" at the Narrows of Newport River.

It is interesting to note that the water at the Narrows

---

[1] Published by permission of the Commissioner of Fisheries.

is markedly brackish, owing to the large amount of fresh water brought down by the river. This, coming from the cypress swamps a few miles away, has a decidedly yellowish tinge, the so-called "juniper water." In density this water ranges from 1.0072 just after one of the tropical downpours to which Beaufort is subject, to 1.0184 when only the normal amount of fresh water is brought down. Ten observations for last summer, which was a normal one from the standpoint of rainfall, give an average density of 1.0153. The average temperature of the water at the time of these observations was 23.6° C. at a depth of three to five feet.

From May 26 to June 12 we constantly caught large numbers of small menhaden, *Brevoortia tyrannus*, averaging about four inches in length. These are probably young of the previous fall spawning. The average size of adult menhaden is about 12 inches. The largest ever taken at Beaufort by the writer was 15 inches long. The record fish for the Atlantic coast is 18 inches in length.

The writer has taken hundreds of gaff topsail catfish at the Narrows, some quite large, but the record was broken on May 27 by the capture of a female, whose length from tip of nose to tip of caudal fin was 24½ inches, and whose girth back of the dorsal was 13 inches. The abdomen was distended balloon fashion by the enormous ovary which occupied almost all of its interior, crowding and displacing the stomach and intestine as it enlarged. This ovisac, after being three days in 10-per-cent. formalin, measured 7½ inches in length and 9¾ inches in girth, and weighed 435 grams.

On May 27, at Cross Rock, we took a large tripletail or flasher, *Lobotes surinamensis.* Its length all over was 25 inches, its depth (body only) 10½ inches. Unfortunately there was at hand no means for weighing it. Other large fish of this kind recorded in the card catalogue at the laboratory are, one 21 inches long and 8½ inches deep, another 18½ inches long, a third 18 inches long. All were taken by the writer; the last in the pound net two miles up Newport River, the others at the Narrows. Smith in his "Fishes of North Carolina"[2] notes three large specimens from Beaufort: one of 25 inches, another of 23 inches, and a third (length not given) which weighed 11 pounds.

On May 31, a 14⅛ inch specimen of the cutlass-fish, *Trichiurus lepturus,* was taken at Rockfish Rock. On June 5, another specimen, 15¾ inches long over all, was taken at the same place. These young fish showed clearly the oral breathing valve, which is perhaps more plainly seen in the mouth of the adult than in any other fish known to the writer. One of these fish had had a bite taken out of its dorsal fin and region just over the hinder edge of the pectorals. This has failed to regenerate and the wound had healed, leaving a crescent cut out of the fin.

Not only are these the smallest specimens of this fish ever taken at Beaufort, but they are further interesting because of the fact that both so amply justify the name "hair-tail," since in each the tail is prolonged backward in a long delicate whiplash-like organ, much slenderer in proportion to the size of the body than is the case in the adult. They were probably two, quite certainly not more than three years old. The writer has obtained eggs by "stripping" this fish in August, and sperms from males caught in July. Nothing, I believe, is known of the embryology of the fish, but Lutken,[3] in 1880, figured and described the young of two allied forms, *Gempylus serpens* and *Neolotus tripes.*

On the same date and at the same place as the preceding, there were taken four specimens of the cow-nosed ray, *Rhinoptera bonasus.* These were all about of one size, averaging 24 inches wide. A female after being clubbed on the head until insensible, gave birth, while being cut open, to two young measuring 8½ inches long and 13½ inches wide. This premature delivery of the young, brought about by muscular contraction due to reflex action, is by no means unusual, the writer having noticed it on several occasions in both butterfly and sting rays. Not infrequently, however, the young are born while the mother is being killed, the pain causing spasmodic contractions of the muscles of the uterus.

---

[2] Smith, H. M., "The Fishes of North Carolina," N. C. Geological and Economic Survey, Raleigh, 1907.

[3] Lutken, Chr., "Spoila Atlantica," *Danske Videnskabernes Selskabs Skrifter,* 5te Raekke, Natur. og. Math. Afdeling, Table III., figures 3–8.

In this connection it is interesting to read in Schomburgk[4] as follows:

> I have frequently observed that the rays, no doubt in consequence of the anguish when secured and transfixed by the poles (harpoons), brought forth their young ones.

A similar occurrence was once noticed by Dr. S. Westray Battle, of Asheville, N. C., who related it to the writer. The young slip very readily out through the genital orifice, and on several occasions (July 29, 1902, for the first time), I have delivered the mother of her young by manipulating her abdomen in the manner familiar to spawn takers. The young are rolled up in tubes, one pectoral fin forming the inner lining of the tube, the other the outer; *i. e.*, the fish is rolled up like a sheet of paper beginning at the edge of one pectoral. It is interesting to note that the teeth of these young rays were hard and fit for service, and the spines able to produce a wound.

On May 29 I found on Fort Macon Beach, about one half mile south of the concrete breakwater, a dead and half dried specimen of *Raja eglanteria*, called "brier ray" because of the curved prickles with which its dorsal region and especially its tail are covered. This is the "clear-nose" of the fishermen, and the dried specimen in question fully justified the appellation, since the membrane joining the rostral cartilages to the pectoral fins was translucent almost to the point of transparency. The fontanelles of the skull, especially the anterior one, were clearly marked out. The total length of this specimen from tip of nose to broken-off end of the tail was 19 inches: the pectorals were rolled up and so hard that it was impracticable to ascertain the width of the fish.

This is the only specimen of the ray which the writer has seen, and the only one noted in the card catalogue at the laboratory. Of this species, Smith[5] wrote in 1907:

---

[4] Schomburgk, R. H., "Fishes of Guiana," Part II., in Jardine's Naturalist's Library, 1843.

> It has not previously been recorded from North Carolina, although it doubtless occurs along the entire coast of the state. At Cape Lookout, on April 22, 1904, the author observed numerous specimens on the beach and was informed that many are caught in the deep-water gill nets set in that region.

On June 5 a three-foot male *Scoliodon terranovæ,* the ordinary sharp-nosed shark found everywhere in the harbor, was captured at Lawton's Rock. Noticing that he had the tail of an ordinary eel, *Anguilla chrisypa,* sticking out of his mouth, I opened him and found in his stomach the half-digested remains of two other eels, smaller than the first. This observation leads one to conjecture whether eels constitute a steady article of diet for sharp-nosed sharks.

Lest it should seem strange for the shark to be taken and to die in the boat with this half-eaten fragment of food in his mouth, it may be of interest to add that I have seen in the hold of a menhaden schooner, sharks of the same kind literally full of menhaden, stomach, gullet and mouth; and with menhaden impaled on the teeth half in and half out of the closed mouth. The menhaden fishermen report that this is a very common experience with them.

The spotted sting ray, *Aëtobatus narinari,* was first described from Brazil by George Marcgrave in his "Historiæ Rerum Naturalium Braziliæ," published in "Historia Naturalis Braziliæ" by William Piso and George Marcgrave at Lugduni Batavorum et Amstelodami, in 1648. In his description of this ray, Marcgrave gives a figure which is perfectly recognizable and indeed is admirable, considering the time when it was drawn.

Yarrow[6] reports that in his day this ray was very common at Beaufort. But so rare is this fish there at the present time that, in seven summers' fishing, I had never seen one until a female was taken at Rockfish Rock on

---

[5] Smith, H. M., *op. cit.*

[6] Yarrow, "Notes on the Natural History of Fort Macon, North Carolina, and Vicinity," No. 3—Fishes, *Proc. Acad. Nat. Sci. Philadelphia,* Vol. XXIX, 1887.

June 12, and then I was quite sure that I had found a new species until the director of the laboratory, Mr. Henry D. Aller, positively identified it under the above name. Its width across the utmost reach of the pectorals was 26 inches; length, end of snout to tip of ventrals, 18 inches; length of tail, root to tip, 40½ inches; tail with two spines, length over all 56½ inches (tail inserted between bases of ventrals); width between eyes 4 inches.

The most interesting thing about this ray apart from its color is the very unusual structure of its jaws. Whereas, in ordinary rays with pavement teeth, the upper and lower jaws are practically duplicates, in this ray while the upper jaw is of the ordinary shape, the lower is drawn out into a tongue-shaped organ protruding beyond the lips. These would seem to be especially fitted for cracking clams, which dissection proved to constitute its chief food. It should be remarked in passing that the jaws of *Aëtobatus* are noticeably smaller than the jaws of an ordinary ray of the same size.

On July 3 Mr. Russell J. Coles, of Danville, Va., caught in the bight of Cape Lookout and very kindly brought to the laboratory another ray of this species. This was also a female whose measurements were as follows: Width, 23½ inches; length, body only, 16 inches tail, 35½ inches long and provided with two spines; width between eyes, 3½ inches. Mr. Coles, notwithstanding his long experience as a fisherman for sharks and rays at Beaufort and Cape Lookout, thought that he too had caught a new species.

As a further evidence of the scarcity of this ray in the Beaufort region, it may be noticed that the card catalogue of the laboratory has records of but two other specimens. In 1901 some fishermen took on the outer or channel side of Shark Shoal, in the deepest part of Beaufort Harbor an *Aëtobatus narinari* whose dimensions were as follows: Width, 4 feet; length, nose to ventrals, 2 feet and 2 inches; tail, 4 feet and 8 inches long; total length about 6 feet and 6 inches (allow for insertion of tail between ventrals). On August 3, 1909, Mr. C. F. Silvester, of Princeton, N. J., took a specimen inside the hook of Cape Lookout. Of this, however, no measurements were made.

Considerable numbers of sting and butterfly rays, *Dasyatis say* and *Pteroplatea maclura,* were taken at the Narrows. The females of these were commonly found to have gravid uteri. At the beginning of my season's seining, the eggs had on them young in very early stages not longer than 10–12 millimeters, the "selachian stages" of Alcock. Two eggs were found having what seemed to be membranous egg shells like those found on teleost ova, and one had the ends twisted into chalaza-like structures similar to those in a hen's egg. Alcock seems to have found similar structures in *Carcharias melanopterus,* a viviparous shark of the Indian Ocean. He writes:

> Each young one lay, head forwards, in its own separate compartment of the uterus, in which, further, it was completely enveloped in a very delicate membrane of its own. This delicate envelope is evidently the pseudamnion of Parker, which, according to that author, corresponds with the horny egg-shell of viviparous Elasmobranchs.

Those uteri, which contained embryos having the yolk sac gone or reduced to a mere string, had their whole inner surface crowded with villi, shaggy with them. Both the villi and the deeper layers of the uteri were tremendously vascularized, and the whole uterus in any specimen was greatly distended by this unwonted blood supply. Uteri containing young as above described were filled with and had the young bathed in a milky fluid evidently secreted by the villi (in the absence of a placenta) as nourishment for the embryos until the time of hatching. According to Alcock[7] this "milk" is taken through the open spiracles of the Indian *Pteroplatea micrura,* a closely allied form, into the mouth, stomach and intestine. Since the Beaufort species likewise have the spiracles wide open, it is fair to suppose that they too feed in the same way. This fluid, somewhat creamy in appearance, was greasy to the touch, and readily coagulated when put into preserving fluids like formalin. I regret that no particular microscopical examination of this "milk" was made. These observations fully confirm those of Alcock[8] on Indian Ocean rays in the "Investigator" expeditions. They are necessarily incomplete, but it is the purpose of the writer to make a careful study of the phenomenon of viviparity in sharks and rays.

---

[7] Alcock, A. W., "Zoological Gleanings from the Royal Indian Marine Survey Ship Investigator." "Scientific Memoirs by Medical Officers of the Army India," Part 12, 1901.

Lepisosteus osseus, the "shell gar" of the fishermen (so called to distinguish it from the green gar, *Tylosurus marinus*, formerly *Belone longirostris*), often comes down from the swamps and upper reaches of Newport River into the brackish water at and even below the Narrows.

In 1908 my fishermen caught several at Cross Rock. Of these, three were thrown on the grated bottom of the gasoline launch, and, with no further attention than having an occasional drenching with a bucket of *salt* water and being covered from the sun's rays by the corner of an old sail, were brought to the laboratory. Here they were put in a large tank of fresh water, which was aerated only semi-occasionally by a jet from a pet-cock. As a result of this severe experience, one of the fish died. However, the other two survived, though their pectoral and caudal fins were badly split and were congested with blood as a result of their threshing around on the floor of the boat during the journey of more than an hour from the fishing ground to the laboratory. Further, in a short time the fins of the living fish became much worn by contact with the scaling paint of the tank.

These two gars came safely through the winter of 1908–09, thanks to the care given them by the laboratory men under the direction of the superintendent of the station, Mr. Henry D. Aller. On my return to Beaufort on May 26, 1909, I found that the fish had completely regenerated their fins and that these were in as good physical condition as the day, ten months before, when the gars were taken out of the bunt of the seine. However, the larger of the two had the body curved in a curious very flat S, which led me to think that it had suffered some injury resulting in deformity. On June 4 this crook had disappeared and the fish seemed to be perfectly normal. Later in the day my attention was called by one of the laboratory men to some spawn floating near the bottom of the tank. This was examined and found to have a greenish color, and undoubtedly was the eggs of one of the gars, presumably the larger. The crook in the body of this fish was probably the result of an effort on her part to rid herself of the eggs without the aid of the sexual excitement engendered by the presence and activity of a male as noted by Dean.[9] The eggs had gone bad—strong evidence that the smaller fish was also a female. When I left Beaufort, at the end of the first week in July, the fish were in prime condition.

---

[8] Alcock, A. W., *op. cit.*; "A Naturalist on Indian Seas," 1902.

Although the water in the tank (size 3 feet by 8) in which the fish were confined, was not more than six inches deep and was aerated only semi-occasionally, the fish did not seem to suffer, thanks to their vascularized air bladders. I watched these gars at irregular but fairly frequent intervals during my six weeks' stay, and noticed that the larger fish seldom came to the surface for air, but that one was quite sure in a few minutes' watching to see the smaller do so. Certain preliminary symptoms always preceded this action: the fish would swim around slowly but uneasily, would shake its head from side to side, would raise its snout nearly to the surface of the water and then sink down; finally with almost imperceptible rapidity the snout would be thrust out of the water and the jaws would open and shut with a convulsive snap; then, as the fish slowly sank to the bottom of the tank, the gill covers would expand and one or two large bubbles of air would escape from under each operculum.

The fish were fed simply by putting into the tank live minnows, chiefly *Fundulus*. These seemed much frightened and would huddle in a corner of the tank as far from the gars as possible. In feeding, a gar would slowly swim behind a *Fundulus*, make a sudden dash, and seize it crosswise in its long toothed jaw. Then elevating its head, possibly out of water, with a quick jerk the gar would catch the fish head first and speedily swallow it.

---

[9] Dean, Bashford, "The Early Development of Garpike and Sturgeon," *Journal of Morphology*, Vol. 11, 1895–96.

ON THE EFFECT OF EXTERNAL CONDITIONS ON THE REPRODUCTION OF DAPHNIA [1]

DR. J. F. McCLENDON

CORNELL MEDICAL COLLEGE

SINCE in the great majority of organisms only the germ cells are capable of reproducing the entire individual, the question as to what differences exist between the germ and body cells, and how they arise, is of general interest. Therefore any change of conditions which affects the germ cells or their relation to the body cells deserves special study. In *Daphnia* external conditions not only affect the relation of the germ cells to the body cells, but they affect the egg cells in such a manner as to determine whether they do or do not need fertilization. The purpose of the present paper is not merely to add the results of my experiments to those of other investigators, but to tentatively arrange the available data under a general working hypothesis in the hope that some more direct method of investigating the relation of the germ and body cells be devised.

Last spring (March 10) I began experiments on the effects of environment on *Daphnia pulex,* De Geer, without knowing that Woltereck was working on the same line. The material came from a small pool investigated by Dr. W. C. Curtis and containing a single strain of this and no other species of *Daphnia.* For the first few weeks some ice remained on the pool and the temperature did not much exceed 4° C.; after this it rose steadily to about 20° by the end of May. Specimens from the pool were examined at intervals as a control on the experiments.[2]

---

[1] From the Zoological Laboratory of the University of Missouri and the Histological Laboratory of Cornell University Medical College, New York City.

[2] When the daphnids were crowded in dishes of the same pool water they soon began to die, owing to the accumulation of their excretions. When

EFFECT OF ENVIRONMENT ON DIFFERENTIAL GROWTH

By differential growth I mean the unequal growth of different parts, viz., the germ and body cells. Only parthenogenetic females were used, and each was kept separately in the same quantity of water. All measurements were made at sexual maturity, *i. e.*, when the first eggs appeared in the brood pouch. Warren[3] found that under uniform conditions there was a slight variability, but Woltereck showed that these fluctuating variations were very small, though he did find mutations as rare occurrences.

Nutrition.—I had in the laboratory a pure culture of a unicellular green alga which the daphnids ate readily. This alga did not remain entirely suspended in the water, but as the daphnids fed on the bottom as well as while swimming, and stirred up the algæ, it can not be said that most of the food was out of their reach.

Those with a superabundance of food were larger at sexual maturity and had a shorter spine than those with insufficient food, and conversely. The smaller size and longer spine of the starved daphnids are characteristic of immature stages.

Temperature.—Three sets of experiments were

---

transferred suddenly to artesian tap water many died, though with a gradual change all lived. The composition of the tap water was as follows: Ca, $.148 \times 10^{-8}$ molecular; Mg, $.1 \times 10^{-8}$ molecular; CO_3, $.045 \times 10^{-8}$ molecular; SO_4, $.146 \times 10^{-8}$ molecular; Cl, $.055 \times 10^{-8}$ molecular. Besides these were very small quantities of silica, clay, iron, ammonia and nitrates, and traces of lithium and potassium. Beside the carbonates the water when drawn from the tap was super-saturated with carbon dioxide. In order to find the cause of death from change of water I added various amounts of molecular solutions of certain salts. The toxicity of cations increased as follows: $NA < 1/2\,Ca < K$, and of anions: $Cl < 1/2\,SO_4 < HCO_3 < 1/2\,HPO_4$. But as K became toxic only on 1/100 and HPO_4 on 1/500 molecular concentration there must be other toxic substances than salts in the water. The carbon dioxide in the water killed crayfish and was probably the most toxic constituent to the daphnids.

[3] "An Observation on Inheritance in Parthenogenesis," *Proc. Roy. Soc. London*, 1899, LXV, and "On the Reactions of *Daphnia magna* to certain changes in Environment," *Quart. Jour. Micr. Sc.*, 1900.

started: at 4–10°, 19–20° and 29–31° C. The results were as follows:

	Average Body Length.	Ratio of Average Spine Length to Body Length.	Time from Hatching to Sexual Maturity.
4–10°	22	0.24	35 days
19-21°	20	0.25	14 "
29–31°	17.7	0.27	6 "

1 unit = $\frac{2}{27}$ millimeters.

All were given a surplus of food daily. It may be observed that a higher temperature has the same effect as insufficient food.

Salts.—Since salts have such a marked effect on the development of marine and some fresh-water animals, I placed daphnids in the strongest solutions of various salts that they would live in (without acclimatization). The effects in two months (four generations) were unnoticeable.

Light.—Cultures were kept in the dark and in diffuse and direct sunlight, but no effect was observed.

A number of observers have recorded season-polymorphism in daphnids. Wesenberg-Lund[4] pointed out that when the specific gravity and consequent buoyancy of the water decreased—by heat in summer—the body of the daphnids became smaller or were provided with outgrowths, so as to offer a greater resistance to sinking. Wolfgang Ostwald[5] produced, all at the same time, the forms that occurred in nature at different seasons, by varying the temperature. He emphasized the fact that rise in temperature lowered the internal viscosity of the water. He found that in the warm cultures the daphnids often became productive at an undeveloped stage and, as is true generally, reproduction retarded body growth.

[4] "Ueber das Abhängigkeitsverhältnis zwischen den Bau der Planktonorganismen und den specifischen Gewicht des Süsswassers," *Biol. Centlb.*, 1900, XX, pp. 606–619, 644–656, and "Studier over de Danske söers Plankton," Copenhagen, 1904.

[5] "Experimentelle Untersuchungen über den Saisonpolymorphismus bei Daphniden," *Archiv f. Entwicklungsmech. d. Organismen*, 1904, XVII, p. 415.

Woltereck[6] maintains that Ostwald's results were due to the fact that at a higher temperature the daphnids need more food. Woltereck caused decrease in body length both by starving and by increasing the temperature, but the latter was not effective with an optimum supply of food. He found that more food than the optimum produced effects similar to starving. Raising the internal viscosity of the water by adding quince gum produced no effect. He showed that though feeding influenced the differential growth, there was a cyclical tendency for this to vary, viz., season-polymorphism. However, the effects of prolonged abundant feeding were inherited to some degree.

One might interpret these results in different ways. It is known that the temperature coefficients for various chemical reactions are slightly different. Possibly the mean of the temperature coefficients for the processes in the development of the reproductive organs is higher than the same for the body wall, and at a higher temperature the germ cells would develop faster. However, under adverse conditions the "affinity" of the reproductive organs for nutriment is greater than that of the rest of the body, so with deficient food the body wall is retarded more than the germ cells in development. The higher temperature may be considered an adverse condition since the mortality is greater. In this way starving has the same effect as a higher temperature.

Langerhans[7] found that accumulation of excretions caused shortening of the spine in daphnids. I do not know what relation this bears to the above results.

---

[6] "Ueber naturliche und kunstliche Varietätenbildung bei Daphniden." *Verh. Deutsch. Zool. Gesell.*, 1908, p. 234; and "Weitere experimentelle Untersuchungen über Artveranderung, speziell über das Wesen quantitativer Artunterschiede bei Daphniden," *ibid.*, 1909, p. 110.

[7] "Ueber experimentelle Untersuchungen zu Fragen der Fortpflanzung, Variation und Vererbung bei Daphniden," *Verh. Deutsch. Zool. Gesell.*, 1909, p. 281.

Effect of Environment on the Life Cycle

In most species of daphnids, generations of parthenogenetic females alternate with generations of males and females which produce eggs that must be fertilized, and either frozen, dried or kept a long time before they will develop (resting or ''winter'' eggs). In different species the number of successive parthenogenetic generations varies. In some all are, and in some none are, parthenogenetic.

I found that heat hastened the appearance of sexual forms, as did starving or the accumulation of excretory products. All of these factors might be combined in the drying up of a pond, as heat would aid in drying, and drying would concentrate the daphnids and their excretions, and concentration of the daphnids would cause them to eat up the algæ faster than they could multiply. However, by keeping the culture cold, fresh or well-fed, or all combined, I could delay but not prevent the appearance of sexual forms.

Kurz[8] said the drying up of the water caused the appearance of sexual forms, and Schmankewitz[9] suggested that it was the increase in salts. Weismann[10] tested both of these hypotheses and concluded that they were wrong. He also tried the effect of food and temperature, with varying results. He concluded that the life cycle was fixed for each species and variety. Issakowitz[11] concluded that cold favored the appearance of sexual forms and warmth favored the parthenogenetic. Also, hunger favored the appearance of sexual forms and abundant food the parthenogenetic. It may be that cold retarded multiplication of the food plant or the movements of the daphnids so that they did not keep the algæ stirred up in the water sufficiently to get at them. The parthenogenetic egg arises from four cells, but a large number of cells enter into the composition of the fertilizable egg. If the latter egg is not fertilized it is absorbed and, as Issakowitsch noted, furnishes food for the development of parthenogenetic eggs.

---

[8] ''Dodekas neuer Cladoceren nebst einer kurzen übersicht der Cladocerenfauna Böhmens,'' *Sitz. Ber. math. naturw. Wien*, 1875.

[9] ''Zur Kenntnis des Einflusses der ausseren Lebensbedingungen auf die Organisation der Tiere,'' *Zeit. wiss. Zool.*, 1877, XXIX.

[10] ''Beiträge zur Naturgeschichte der Daphnoiden, VII,'' *Zeits. wiss. Zool.*, XXXIII, p. 111.

[11] ''Geschlechtbestimmende Ursachen bei den Daphniden,'' *Biol. Centralb.*, 1909, XXV, pp. 529–536.

Woltereck[12] found that starving hastened the appearance of sexual reproduction, but a concentration of food above the optimum produced results similar to starving. He found, as Weismann maintained, a cyclical tendency toward the alternation of sexual and parthenogenetic generations which, contrary to Weismann, was temporarily influenced by nutrition, and the effects of constant nutrition over a long period was inherited to some extent.

Langerhans[13] found that the accumulation of excretions caused the decrease in numbers of parthenogenetic females in the autumn and thinks that the appearance of sexual forms is due to the same cause.

The life cycle of a daphnid is, therefore, an hereditary tendency, but can be influenced by nutrition and probably by temperature and the accumulation of excretions. Nutrition is the most important factor, and former experiments on the effect of temperature and the drying up of the water were complicated by secondary effects on concentration of food and excretory products.

Discussion of Results.—Two views might be held as to the origin of the differences between the germ and body cells: the differences might be the result of difference in position in the embryo, or of unequal mitoses. In the parasitic copepods I found the primary germ cell to arise by an unequal mitosis at the fifth cleavage of the egg. The germ cell when first formed is one thirty-second of the total number of cells, but owing to the more rapid division of the body cells this ratio decreases. In fact the chief difference between the yolk-free body cells and the (yolk-free) germ cells is the slow rate of division of the latter. Finally, the *eggs* will not divide at all unless specially stimulated, by fertilization. The question now arises: what causes the cell to divide. Sacks found that plant cells divide when they have reached a certain size. This rule has been extended to animals, and the final size of the cell found to be determined by the ratio of nucleus to cytoplasm. This rule may apply to the germ cells, since it appears that after the egg cell, primary oocyte, reaches a certain size any additional food absorbed does not cause growth of the protoplasm, but is precipitated as yolk.

---

[12] *Loc. cit.*

[13] *Loc cit.*

If the egg is properly stimulated, rapid growth of protoplasm and cell divisions follow. From the study of artificial parthenogenesis it appears probable that stimuli which lead to development of the egg increases the permeability of its plasma membrane. If this be true we may say that the germ cells are distinguished by the fact that their plasma membranes are poorly permeable and retard those reactions between the cell contents and environment which lead to growth and cell division. In other words, the optimum intensity of stimulation toward growth and division is higher for the germ cells than for the body cells.

This difference is probably due to a difference in the colloids of the cell, which in animals could be explained as the result of an unequal mitosis. This explanation may be modified so as to apply to plants. Klebs has shown that those conditions which are adverse to vegetative growth of plants (too strong stimuli?) call forth flowers. Perhaps there are slight differences in the sensitiveness of plant cells to stimuli, and as the stimuli increase, those initially least sensitive cells acquire further immunity to the stimulus, whereas those initially more sensitive cells are overstimulated and weakened. Thus the difference between germ and body cells is gradually acquired. The Malpighian layer of the skin may be stimulated to proliferate more rapidly, but if the stimuli are too strong the growth will be retarded instead of increased. On gradually increasing the stimulus immunity to it may be acquired.

To apply this hypothesis to the daphnids: conditions which are adverse to the growth of the body cells, such as extremes of temperature (viz., high temperatures) or of concentration of excretory products, or disorded nutrition, either fail to retard the development of the germ cells or stimulate their development, so that in either case the daphnid becomes sexually mature at a less developed stage. Under the less extreme conditions the eggs develop on receiving the slight stimulus incident to their transfer to the brood pouch, but under the more extreme conditions those eggs which develop at all must be stimulated by fertilization before they develop. These two types of eggs may perhaps develop from two kinds of cells, or the sexual egg may arise from the same kind of cell producing the parthenogenetic egg by acquiring an immunity to slight stimuli. Whereas more than one cell goes to make up a single egg; only one nucleus is retained, and it may be said that one cell is the egg cell and the remainder furnish its food.

ARE FLUCTUATIONS INHERITED?[1]

DR. HARRY H. LOVE

CORNELL UNIVERSITY

THE object of this paper is to present certain facts in regard to the inheritance of fluctuations which have been obtained from a study of the common garden pea (*Pisum sativum*). While an experiment was being conducted to study the effect of fertility upon the fluctuating variability of certain characters, data were also obtained to show to what extent these fluctuating characters are inherited. The peas used were a mixed population and not a pure line, and had not been selected for any particular character when the experiment was started.

The belief has long been held that the improvement of animals or plants could be obtained by selecting from the best individuals, or those possessing to the greatest degree the quality desired.

The fact is that at present most of our agricultural breeding and improvement is based upon this belief and this is the method which is most generally followed in practical breeding. This view held sway from the time of the earliest breeders until the appearance of the Mutation Theory by DeVries. It was first stated scientifically by Darwin in his "Origin of Species," for Darwin, after a study of the evidence accumulated, was convinced that the improved breeds had been obtained in this manner. He says:

> We can not suppose that all the breeds were suddenly produced as perfect and as useful as we now see them; indeed, in many cases we know that this has not been their history. The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him. In this sense he may be said to have made for himself useful breeds.[2]

---

[1] Contribution VI, Laboratory Experimental Plant-breeding, Cornell University. The writer expects to follow with a series of articles on the same subject.

[2] "Origin of Species," Chapter 1, p. 35, Murray Edition.

He further states:

> If selection consisted merely in separating some very distinct variety, and breeding from it, the principle would be so obvious as hardly to be worth notice; but its importance consists in the great effect produced by the accumulation in one direction, during successive generations, of differences absolutely inappreciable by an uneducated eye—differences which I for one have vainly attempted to appreciate.[3]

DeVries after much careful experimentation and study of results of agricultural breeding (mainly the results at Svalöf and those of the German breeders) showed that much of the improvement which has occurred was not due to cumulative selection but must be explained in some other manner.

In recent years much careful scientific work has been done along this line to test the action of selection within a pure line and in a mixed population.

The Svalöf Experiment Station has done much in practical plant-breeding to show that, with reference to the cereals especially, the effect of selection went no further than to isolate the pure lines, and when this was accomplished no further gain was made by selection.

Johannsen,[4] working with beans and Jennings[5] with *Paramecium*, have arrived at the same general conclusion which has been summed up by Pearl[6] as follows:

> From a mixed "general" population it is possible by a single selection to isolate pure strains ("pure lines," "homozygote strains," "pure races") which will breed true and not revert to the mean of the general population from which they were isolated, regardless of whether further selection is practised or not. It is impossible to demonstrate any cumulative effect of continued selection within the pure strain. Continued breeding from the extreme individuals of such a pure strain ("fluctuating" variants) does not change the mean of that strain. From these considerations it follows that it will be difficult or impossible to make any definite and permanent change in the mean of a general population simply and solely by continued selection of extreme indi-

---

[3] *Loc. cit.*, p. 36.

[4] "Uber Erblichkeit in Populationen und in reinen Linien," Jena, 1903.

[5] "Heredity, Variation and Evolution in Protozoa, II," Heredity and Variation of Size and Form in *Paramecium* with Studies of Growth, Environmental Action and Selection, *Proc. Amer. Phil. Soc.*, Vol. XVI, pp. 393–546, 1908.

[6] "Is there a Cumulative Effect of Section?" *Abstammungs- und Vererbungslehre*, 2, 1909, H. 4.

viduals, because in the vast majority of cases such individuals will be extreme fluctuating variants rather than mutants.

Jennings[7] states in his paper that "Systematic and continued selection is without effect in a pure race, and in a mixture of races its effect consists in isolating the existing races, not in producing anything new." And concludes[5] that "Until some one can show that selection is effective within pure lines it is only a statement of fact to say that all the experimental evidence we have is against this."

Recently Pearl[6] has brought forth a very noteworthy contribution in this line. His evidence is based upon the work which is being done at the Maine Agricultural Experiment Station to determine the effect of selection on fecundity and the inheritance of fecundity in poultry. His conclusions may be summed up as follows:

> Selection for high egg production carried on for nine consecutive years did not lead to any increase in the average production of the flocks.
>
> The present data give no evidence that there is a sensible correlation between mother and daughter in respect to egg production, or that egg-producing ability (fecundity) is sensibly inherited.
>
> In this experiment the daughters of "200-egg" hens did not exhibit, when kept under the same environmental conditions, such high average egg production as did pullets of the same age which were the daughters of birds whose production was less than 200 eggs per year.

Professor Waugh,[8] of the Massachusetts Agricultural Experiment Station, has been making some studies of the variation of peas and the inheritance of the different fluctuating characters. He has found that the coefficients of heredity for the different characters are very low and are not very significant in the case of any one character. The two characters, length of vine and number of pods per vine, show a coefficient of heredity of .170 and .158, respectively. At the same time he found that there were certain lines that did reproduce their characters to an appreciable extent, which is along the

[7] "Heredity and Variation in Simplest Organisms," AMER. NAT., June, 1909.

[8] Twenty-first Ann. Rept. Mass. Agr. Exp. Sta., Part II.

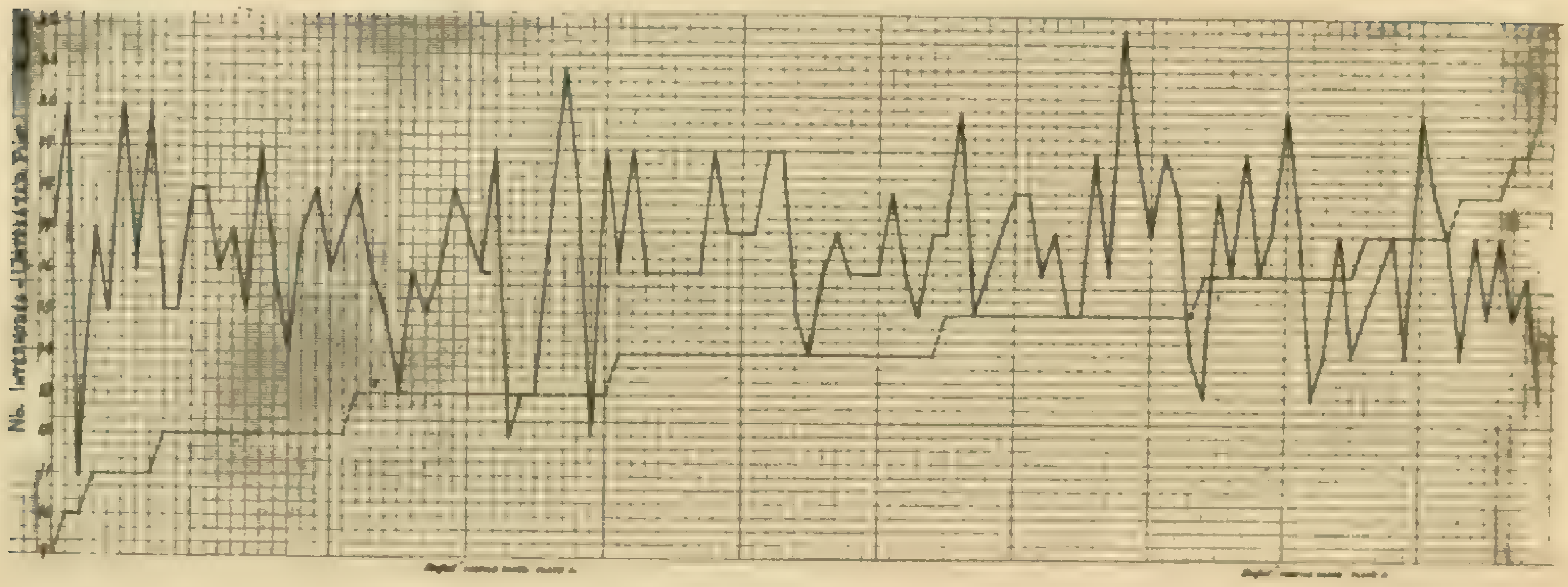


FIG. 1. Diagram showing the relation between parents and offspring in regard to number of internodes on the untreated plot. The broken line represents the parents and the solid line the offspring.

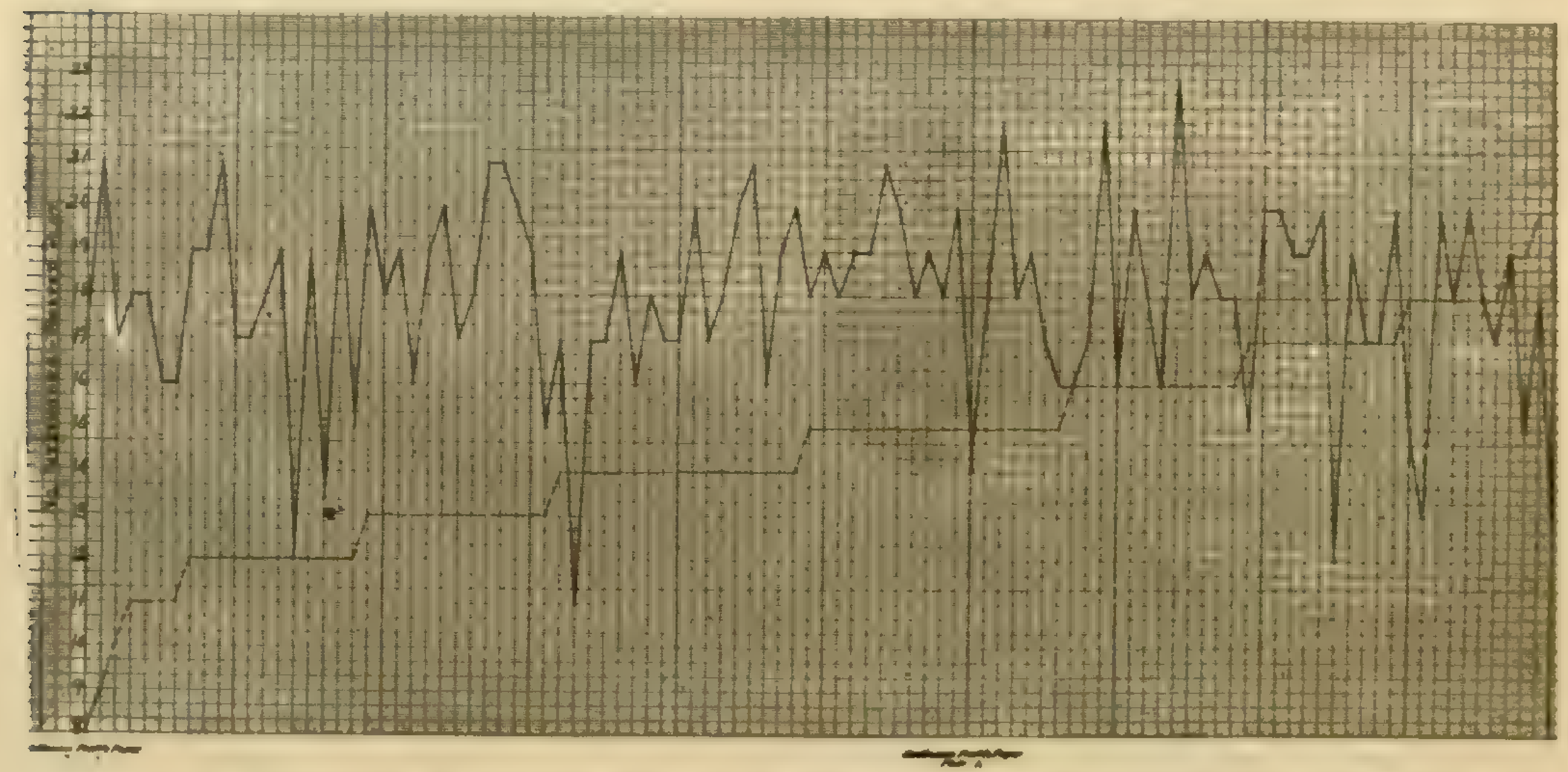


FIG. 2. Diagram showing the relation between parents and offspring in regard to number of internodes on the treated plot. The broken line represents the parents and the solid line the offspring.

line of other studies dealing with pure lines which have been reported.

The evidence which the writer here presents is not based upon large enough numbers to be conclusive in itself, but it is certainly suggestive and adds to the facts already brought together. The number of individuals used is as large as is used many times in the beginning of a practical experiment to develop a strain by selection.

Plan of the Experiment.—The writer studied the variability of peas when grown on plots of different fertility, and in carrying this study on a second generation the planting was done in such a way that the parentage of each plant was known. That is, each plant of the

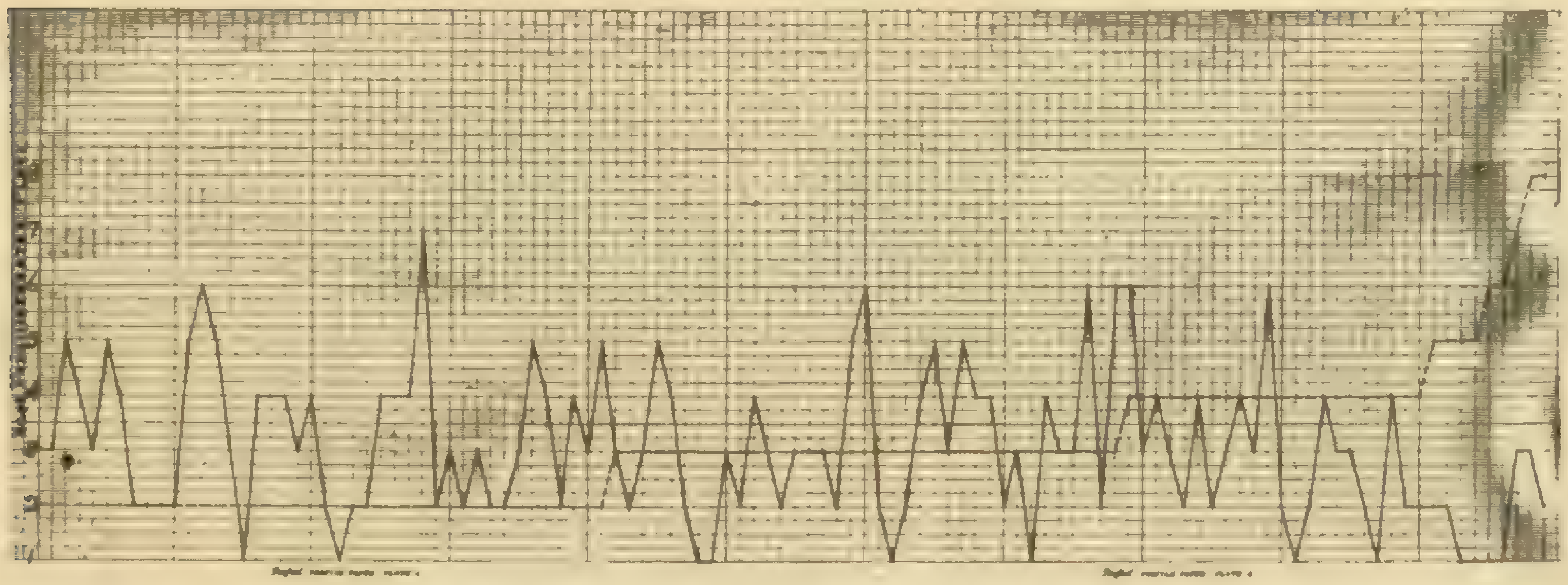


FIG. 3. Diagram showing the relation between parents and offspring in regard to number of pods on the untreated plot. The broken line represents the parents and the solid line the offspring.

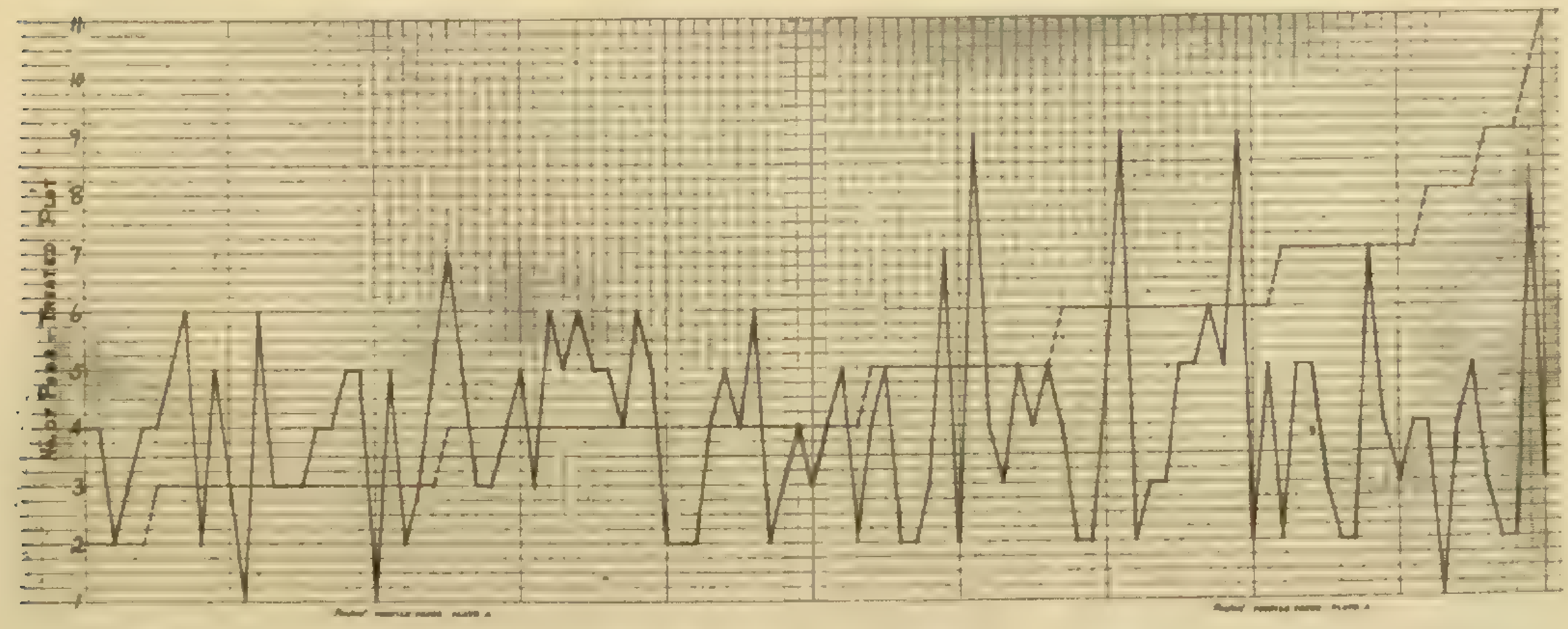


FIG. 4. Diagram showing the relation between parents and offspring in regard to number of pods on the treated plot. The broken line represents the parents and the solid line the offspring.

second generation plants was planted from certain parent plants, and the records were kept in such a way that the characters of the offspring could be compared with those of the parents. As stated above, the number of individuals was of necessity small, yet since the study was made under two different soil environments it seems quite representative of what one is to expect in ordinary selection work.

The difference between this study and regular selection work is that no selection of parents was made, while in ordinary selection work the best individuals are saved for planting.

These data are presented to answer the questions—"What basis have we to expect a cumulative effect of selection? Do we find the resulting offspring following the law of regression?"

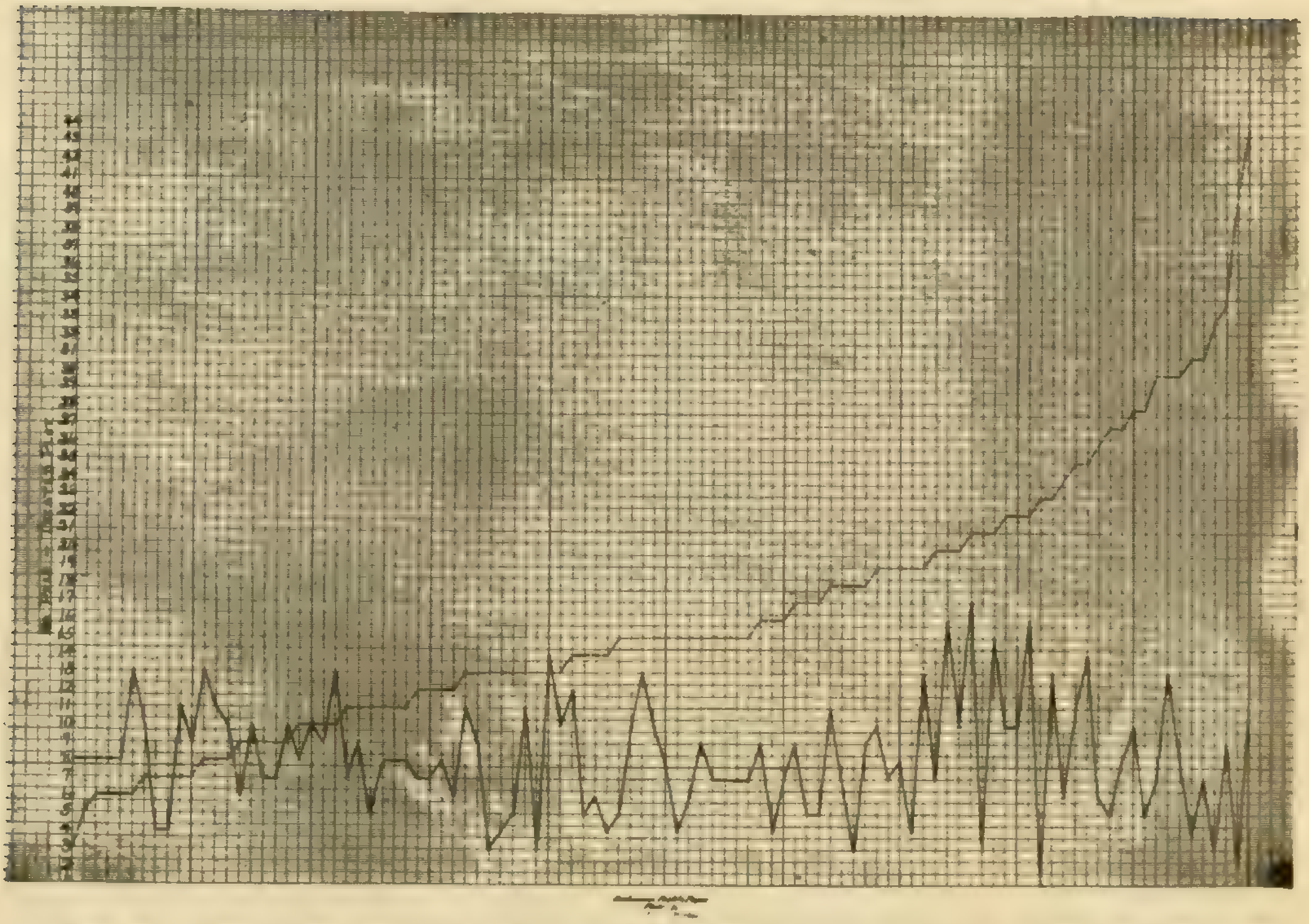


FIG. 5. Diagram showing the relation between parents and offspring in regard to number of peas on the treated plot. The broken line represents the parents and the solid line the offspring.

Regression tables were made for several characters obtained from the plants studied. Such characters as, height of plant, number of internodes, number of pods, number of peas and yield of seed were observed. The results of these calculations are shown in Table I.

TABLE I

Character	Coefficients of Heredity Ordinary Soil Plot	Fertilized Plot
Number of internodes	.027 ± .064	—.050 ± .067
Number pods per plant	—.235 ± .061	.012 ± .067
Number peas per plant	—.152 ± .063	—.045 ± .067
Height of plant	—.191 ± .062	.014 ± .067
Yield of plant (peas in grams)	—.100 ± .064	.001 ± .067

We see that the coefficients of heredity are very low and some of them are even negative. This shows that as far as this data is concerned these fluctuating characters do not follow the law of regression to any appreciable extent. No emphasis should be placed upon the fact that some of these coefficients are negative, but the point is that they are not positive to any noticeable degree. The charts (Figs. 1–9) show in a graphic manner

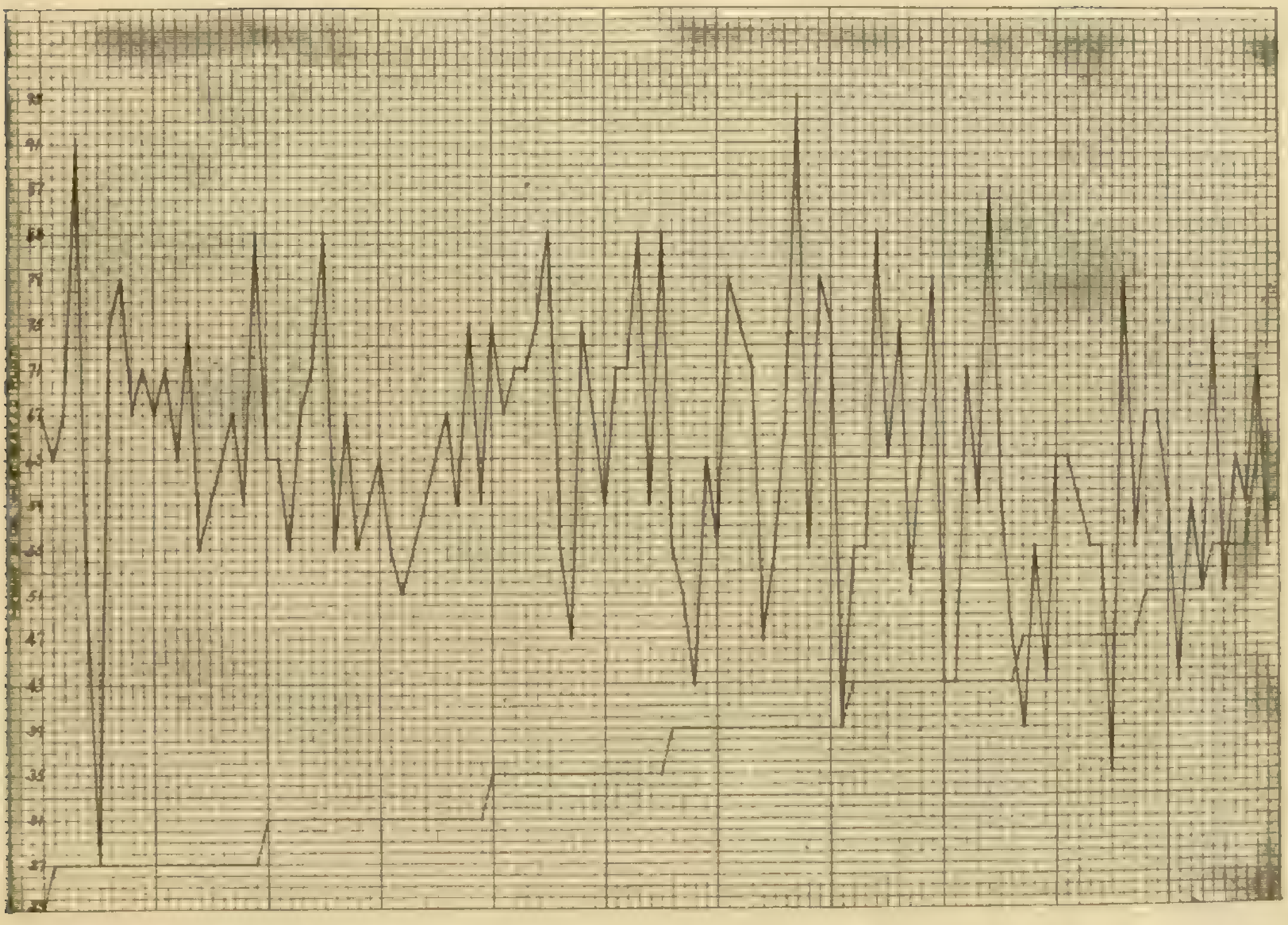


FIG. 6. Diagram showing the relation between parents and offspring in regard to height on the untreated plot. The broken line represents the parents and the solid line the offspring.

the lack of inheritance for these different characters. In each case the dotted line represents the parent plants and the solid line the offspring. These point out some very interesting facts. While we find that in general the coefficients of heredity are practically negligible quantities, yet there are certain parents which reproduce some of their characters. This we are to expect from our knowledge gained by the study of populations. That is, in the study of a mixed population we expect to find certain lines which will reproduce to a marked degree.

The charts show that the line representing the offspring for any certain character seems to rise or fall independently of the value of the parental plant. These diagrams show how in some cases the line for the offspring tends to go down rather than up, but no conclusion must be drawn from this other than that it does not follow the parent line and rise as the parent line does.

Often there arises a question in the minds of those believing in cumulative selection, which may be stated as follows: If we take any population and group it ac-

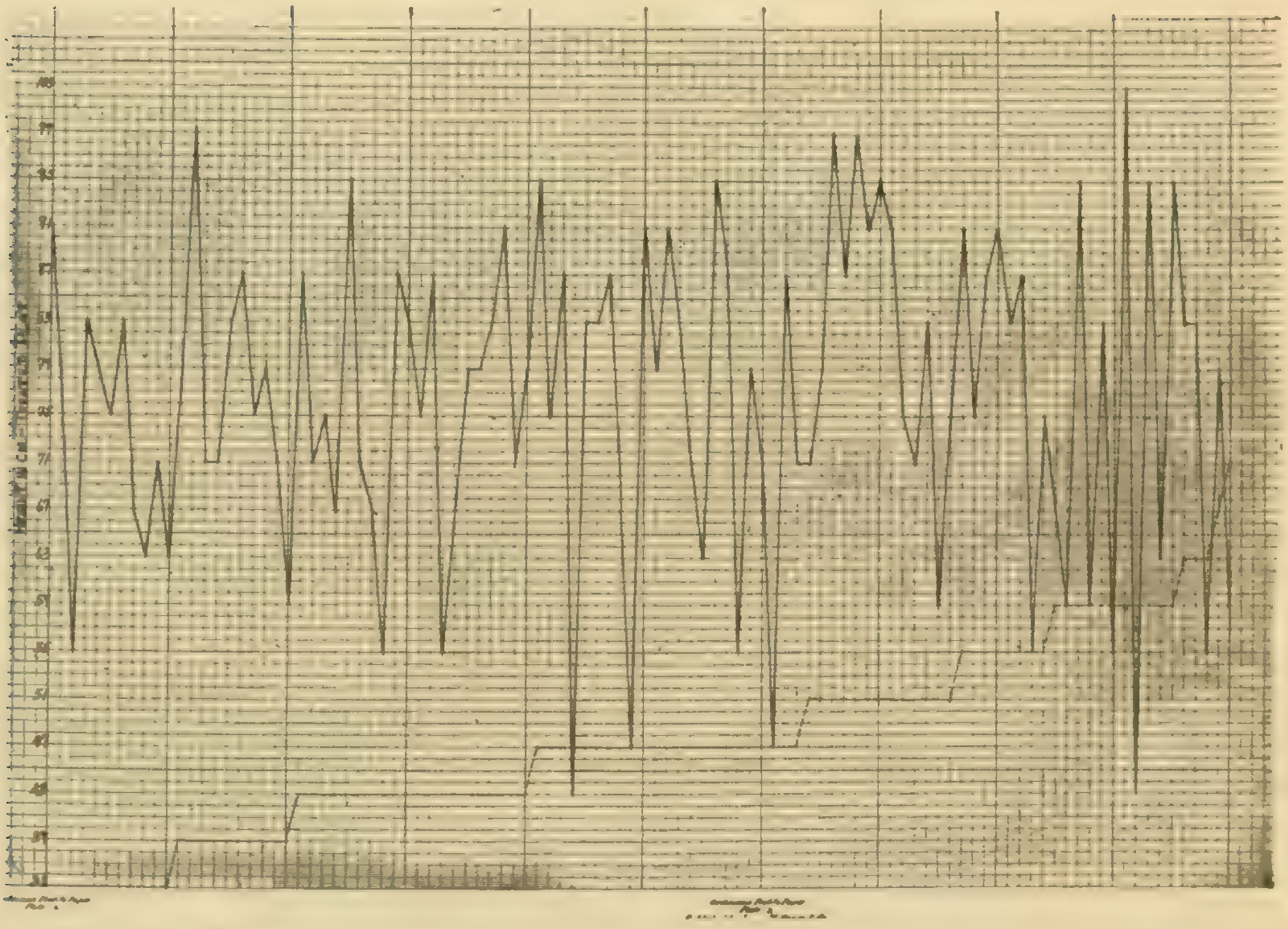


FIG. 7. Diagram showing the relation between parents and offspring in regard to height on the treated plot. The broken line represents the parents and the solid line the offspring.

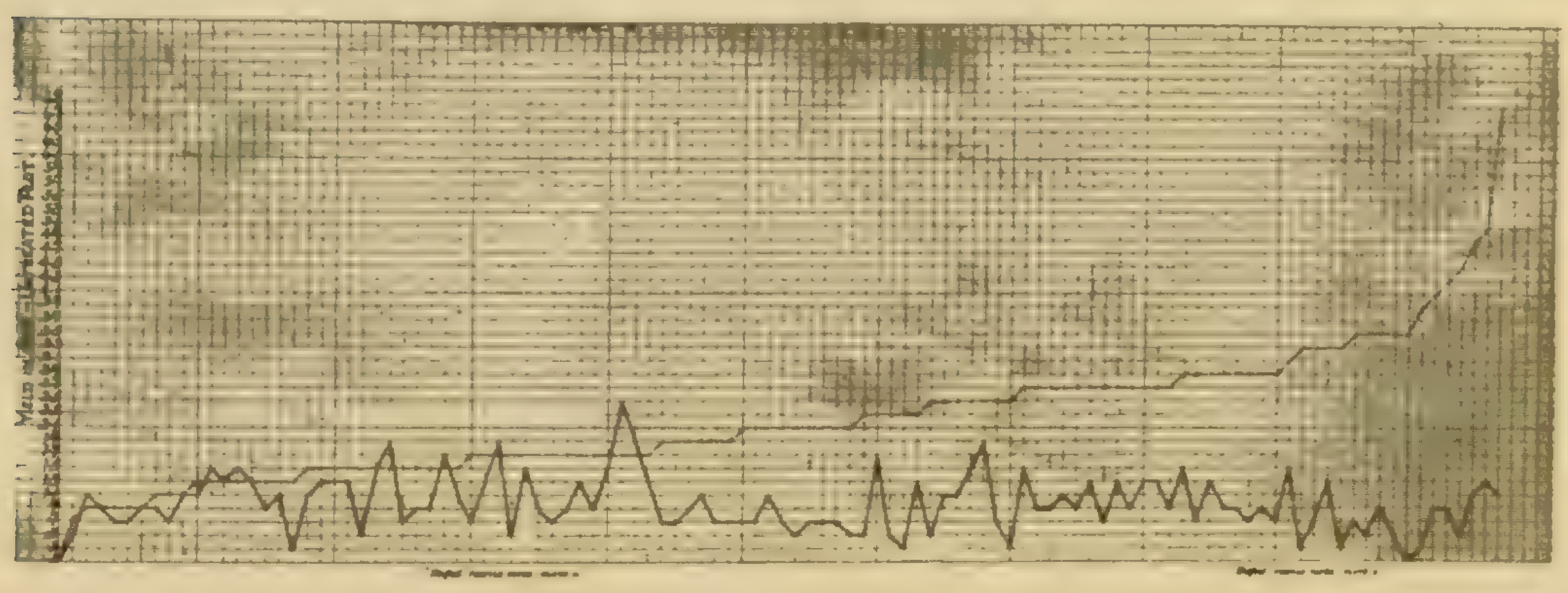


FIG. 8. Diagram showing the relation between parents and offspring in regard to yield on the untreated plot. The broken line represents the parents and the solid line the offspring.

cording to any certain character and select from above or below the mean, will not the progeny resulting from the individuals above the mean possess this character to a greater degree than those coming from parents below the mean?

To answer this the writer has arranged the data in the following manner: The individuals used as parents were divided into two parts, the lower half, or the half possessing the character in question in the least degree,

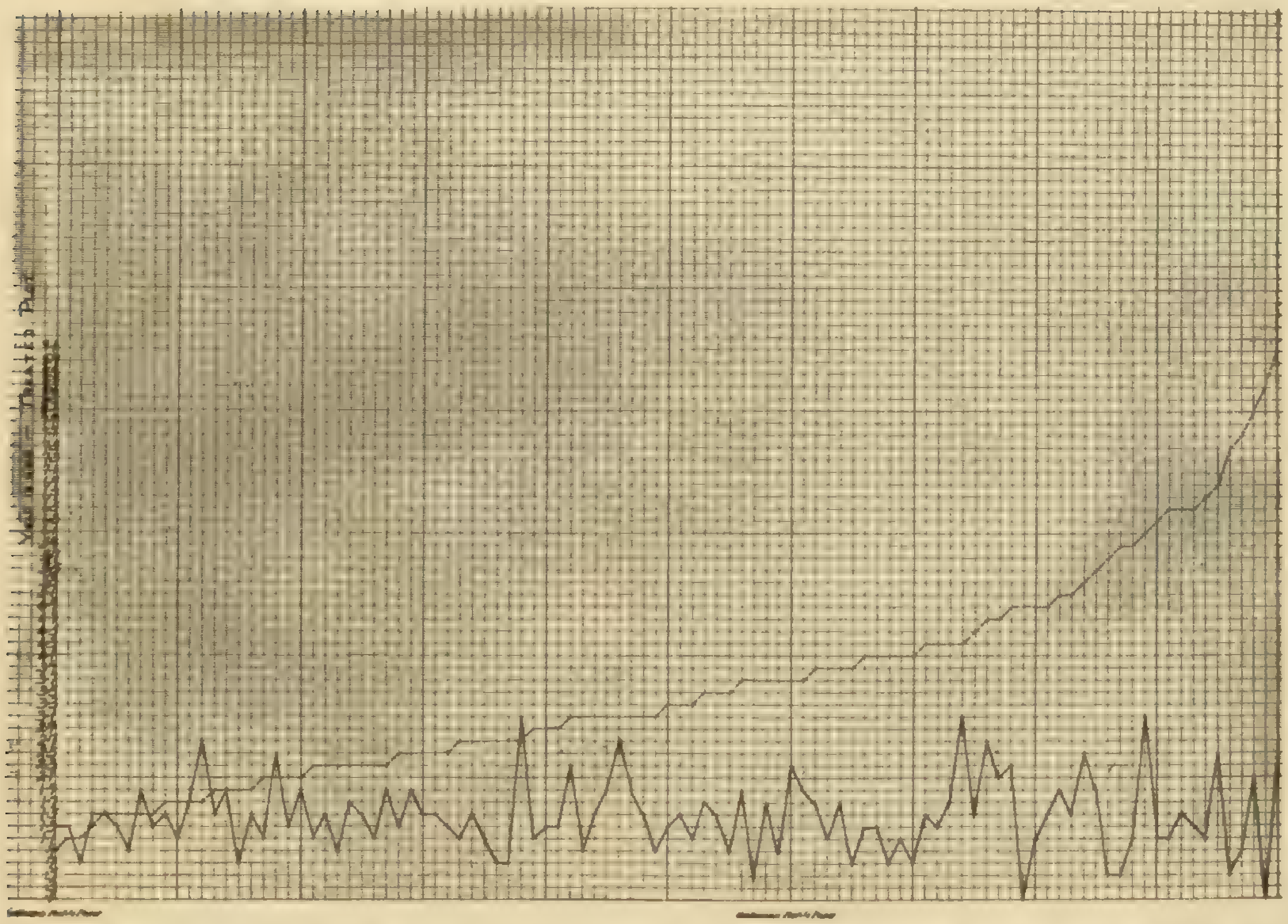


FIG. 9. Diagram showing the relation between parents and offspring in regard to yield on the treated plot. The broken line represents the parents and the solid line the offspring.

and the upper half. The resulting offspring was again averaged for the different characters and the results are shown in Table II.

TABLE II

AVERAGES FOR THE DIFFERENT CHARACTERS

Character.	First Half.		Second Half.	
	Parent.	Offspring.	Parent.	Offspring.
Height, untreated	30.6	65.3	45.0	60.7
" treated	41.2	75.4	53.7	77.7
Internodes, untreated	12.6	16.5	15.8	16.5
" treated	12.8	17.9	16.5	18.0
Number pods, untreated	2.2	3.2	3.9	3.0
" " treated	3.4	3.9	6.3	4.0
Number peas, untreated	6.4	5.9	12.7	4.8
" " treated	10.5	8.3	22.2	8.1
Yield, untreated	1.493	1.048	3.011	.889
" treated	2.260	1.476	4.986	1.453

Again, the individuals were divided into three parts as follows: The first third, or those in which the average of any character for the parents was the lowest, the second or middle third, or those near the mean, and the third third, or those in which the average for the parents was the highest. The average was obtained for the different characters in the offspring produced from these different lots of parents and the results tabulated and shown in Table III.

TABLE III

AVERAGES FOR THE DIFFERENT CHARACTERS

Character.	First Third.		Second Third.		Third Third.	
	Parent.	Off-spring.	Parent.	Off-spring.	Parent.	Off-spring.
Height, untreated	28.7	64.1	36.8	65.4	48.	59.6
" treated	39.2	75.1	46.6	77.1	56.8	77.5
Internodes, untreated	12.1	16.2	14.1	16.8	16.4	16.4
" treated	12.1	17.7	14.6	18.3	17.2	17.8
Number pods, untreated	2.	3.3	2.9	3.1	4.4	2.8
" " treated	3.1	3.9	4.4	4.1	7.1	4.0
Number peas, untreated	5.6	5.6	8.8	5.8	14.2	4.7
" " treated	8.9	8.5	15.	7.3	25.5	8.8
Yield, untreated	1.311	1.044	2.100	.972	3.343	.889
" treated	1.941	1.453	3.335	1.453	5.688	1.488

We see that there is no general increase for the value of the different characters as we pass from the lower half to the upper half, or from the lower third to the middle or upper third. In some instances there is an increase, in others a decrease. That is, the individuals resulting from the parents above the mean do not possess the character to any greater degree than those resulting from parents below the mean. We see then that these data answer the question in the negative; or to take a concrete case, the number of peas per plant on the untreated plot show that plants resulting from the upper half of the parents *do not produce* any more peas per plant than those coming from the lower half. The results are as follows:

Average of Parents	Average of Offspring
6.4	5.9
12.7	4.8

The two tables show very clearly that as far as this data are concerned, there is no difference in the offspring resulting from high or low averaging parents.

As peas are self-fertilized, it will be of interest to note some results obtained with a cross-fertilized crop. The writer has obtained data from selection experiments in corn which are very interesting in this connection. While selecting for yield and earliness data have been obtained which tend to show that corn is not different from peas and that in general fluctuations are not inherited, but that certain individuals reproduce to a high degree. The results obtained with yield are shown in the following table.

TABLE IV

	Average Yield of Parents	Average Yield of Offspring
Plot 1	46.6 lbs. per row	43.0 lbs. per row
Plot 1	52.5 lbs. per row	44.8 lbs. per row
Plot 2	27.2 lbs. per row	81.5 lbs. per row
Plot 2	34.1 lbs. per row	76.2 lbs. per row

While making these studies the effect of the size of seed planted on the offspring was determined. In planting the second generation plants, unfortunately, the seeds were not weighed, but an average seed from each parent was taken and planted. The chances are that by selecting in this manner an average sized seed would be obtained, and since the average weight seed for each parent plant is known, it seems fair to assume that the seed planted approached the average weight of seed. Regression tables were arranged for the two plots in which the height of plant for the offspring was correlated with the average weight of seed for the parent plants. These tables show that as the average weight of seed planted increases, the height or size of the resulting plant also increases. Although the coefficient is not high in either case, yet it is higher on each of the plots taken than that determined for any character. This seems to show that the size of seed, regardless of the plant from which it came, has more influence on the offspring than the parent plant itself. The coefficient is .276 ± .059 for the untreated plot and .139 ± .066 for the treated plot.

Waldron[9] has shown that large (heavy) seed in oats comes from the shorter culms and suggests that in selecting large seed for planting we are selecting from small plants. This may be true. The writer finds that the average weight of seed in peas decreases with the height of plant, which corresponds to the results obtained by Waldron. On the other hand, when these are planted the larger seed, although coming from smaller (shorter) plants, produced larger plants than smaller seed which came from the large plants.

---

[9] "A Suggestion Regarding Heavy and Light Seed Grain," Amer. Nat., Vol. XLIV, January, 1910.

The foregoing results then indicate that there is not enough evidence in favor of the inheritance of fluctuations caused by environment to form a practical working basis. That is, by selecting out the individual plants which give an exceptionally high yield we would not obtain any higher yielding individuals than from a selection taken at random.

We find then that we have given a definite answer to the question which is the title of this paper.

While such statements do not accord with those who place their faith in cumulative selection, yet it is only a statement of fact as shown by an analysis of such data as are here brought together.

These results accord very closely with those stated by Pearl[6] and we can agree with a statement made by him which is as follows:

> Altogether much evidence is accumulating from widely different sources to show that simple selection of superior individuals as breeders can not alone be depended upon to insure definite or continued improvement in a strain. Some improvement may possibly follow this method of breeding at the very start but the limits both in time and amount are very quickly reached.

The rapidly accumulating facts in this respect bring us to face a different view of the value of selection. The testing of individuals to learn their power to reproduce their characters must be done just the same but a different interpretation must be given the results obtained.

Unless further studies produce different results, we can say from the facts at hand that there is no evidence to show that a basis exists for cumulative selection.

INHERITANCE IN POTATOES

PROFESSOR EDWARD M. EAST

Harvard University.

A study of the behavior of certain plant characters in inheritance formed part of an investigation into the factors connected with the improvement of the common potato as a commercial crop, begun at the Connecticut Agricultural Experiment Station in 1906. This work was really a continuation of investigations made by the writer at the University of Illinois from 1902 to 1905, along broader and somewhat different lines. In 1908[1] the many disheartening difficulties attending hybridization were discussed, but it was shown to be possible to overcome several of the obstacles by proper treatment. The conclusions drawn at that time have not been changed by further experience, but the hindrances caused by external conditions not under control have been so great that the work has been discontinued. For example, in 1908 a prolonged drought at the time the fruits were forming, caused one hundred and fifty cross- and self-pollinated seed-berries to drop off while yet too immature for the seed to germinate. Not a single hand-pollinated flower matured its fruit.

Recently, a part of the pedigree records were lost in a fire which destroyed one of the buildings of the Connecticut Agricultural Experiment Station. For these reasons the data reported here do not represent fairly the amount of work done upon the subject, for the actual number of plants under observation was considerably larger than the figures reported. The complete figures had been studied with some care before the loss of the records, and it is thought that the remaining records are a fair sample of the whole.

The records contain observations on only one generation of plants, together with the characters possessed by their parents. I have endeavored to find what characters were possessed by the parents of the varieties used in crossing but have found no trustworthy data. The following conclusions, therefore, are tentative. Nothing is known about the behavior of the characters when extracted. The data show that *certain characters segregate,* they give some evidence as to dominance and recessiveness, but they do not show the exact behavior of the Mendelian factors concerned, under different combinations.

---

[1] Some essential points in potato breeding. Biennial Report, Conn. Agr. Exp. Station, 1907–1908, 429–447, 1908.

Color in the Plant Stem

Many varieties have a purple anthocyan sap color which gives the plant stem a dark appearance quite distinct from the clear green stems of the varieties in which it is absent. The color is variable in amount in different varieties. In some it extends throughout the petioles and petiolules; in others it can only be detected on the stems of the young seedling. My counts were made on seedlings about four inches high.

The color is evidently of the same nature as that found in many other cultivated plants. Its widespread occurrence and seeming uselessness in the plant's economy would place it in the category of typical varietal characters in the sense used by De Vries. It forms a single allelomorphic pair with its absence.

One purple-stemmed variety selfed gave all purple-stemmed progeny. Four purple varieties selfed, each showed segregation into two distinct classes, purple and non-purple. Fifty-four purple plants and seventeen non-purple plants were obtained. (These figures as well as those that follow are the records saved from the fire.) In each of these cases we may take it that the parent plants were heterozygous for the purple color, and approximated the simple three to one Mendelian ratio when self-pollinated. Four green-stemmed varieties were also selfed, and produced nothing but green-stemmed progeny.

One of these pure green-stemmed varieties was crossed on one of the heterozygous purples, and thirteen seedlings were obtained. Six plants were purple-stemmed and seven were green-stemmed. This result is what would be expected when crossing DR × R.

Color in the Flowers

All potato flowers have a ray of yellow extending from the limb of the corolla toward the apex of each lobe. The remainder of the corolla is either white or purple. There is wide zygotic (in potatoes, therefore, varietal) variation in the intensity of the purple sap color, but the flowers should probably be classed as either purple or white. The fact that the variety color, whether light or dark, remains true when propagated asexually, does not necessitate more than one Mendelian pair. It is undoubtedly a quantitative difference in the same pigment which is kept constant by the asexual method. Why somatic cell divisions should reproduce a color shade so exactly, while sexual reproduction gives rise to varying shades is unknown. It is the more peculiar since in animals visible division of the chromatin appears to be much more accurate in the sexual cells than in the somatic cells. The somatic cell appears to have the power of developing and of regenerating only the quantity of color originally apportioned to it, except on the rare occasions when all of the potential color activity goes to one daughter cell and the other is left without it. When this occurs, branches resulting from the descendants of the second cell are "sports" or "bud-variations" in which the original character is lost.

Only two varieties of potatoes with flowers other than purple or white have been noticed. The variety *Holland fleur de June* has blossoms which are decidedly yellow. Several attempts to self this variety and to cross it with other varieties failed. One other variety, a nameless seedling of unknown origin, possessed a true blue flower. No admixture of red which would give it a purple tinge could be detected. Even this color, however, may be of the same nature as the purple color, the difference being in the completeness of the reaction forming the blue dye. It will be remembered that litmus reacts in this manner. Several cross-pollinated and several self-pollinated fruits were obtained from this variety, but none of the seedlings had flowered in 1909, the second year of their growth.

The seedlings of the potato are very slow to flower in a New England environment, and but few flower records were obtained among several hundred plants. One selfed variety with purple flowers gave progeny all with colored flowers. Three selfed varieties with purple flowers gave both purple and white flowers: the total number of seedlings that flowered was nineteen, of which fourteen were purple-flowered and five were white-flowered. Three selfed white-flowered varieties gave nothing but white-flowered progeny.

Since three white-flowered varieties gave nothing but white flowers and three out of four colored varieties showed a hybrid condition with segregation of color, the purple is probably dominant to its absence. Color and no color is probably a single Mendelian pair, but this can not be stated with certainty from such meager data.

COLOR IN THE TUBERS

Potato tubers, when colored,[2] are either purple or red. In both cases the color may extend over the entire tuber or may be limited in extent. No definite mosaic pattern is formed when the color is limited, but the splashes of color are restricted to pretty definite areas. It is probably due to a separate Mendelian factor, for the mosaic varieties and the self-colored varieties are distinct. Tuber color varies quantitatively more than flower color. Many varieties show no color in the skin, and can be classified only by examining the young shoots when the latter are about half an inch in length. The progeny of such varieties belong to the same classes as the progeny of self-colored varieties. They give fewer self-colored seedlings, however, which may be due to the action of one or more unknown heritable factors. I have not attempted to separate the self-colored from those showing color in the young shoots, but have classified both as colored varieties.

---

[2] Colorless skins may vary from white to dark brown in different varieties. This is entirely due to their possessing corky layers of various thicknesses.

The results of selfing varieties with different color characters are as follows:

Selfed purples gave either all purples (one variety); purples, reds and colorless (two varieties); or purples and colorless (three varieties). Selfed reds gave either all reds (two varieties), or reds and colorless (two varieties). Selfed red varieties gave no purple progeny. Three colorless varieties (that is, no color in *either* the *tuber skin* or *young shoots*) were selfed, giving all colorless progeny.

Without considering factors for limiting color, these results seem to show that purple and red are separate Mendelian units, each dominant to its absence, and that purple is epistatic to red.

It is an interesting fact that although the purple varieties and the red varieties are distinct color types without intermediates and that mosaic varieties of each are known, yet in no case has a mosaic variety appeared in which splashes of the two colors are found. We may conclude therefore that the two colors are formed by the action of other factors upon the same chemical constituent. If we assume that the red color is a lower form of oxidation than the purple color and that they are produced by different oxidases R and P acting upon the same substance C, the results obtained are explained, for the presence of P would oxidize all of the stubstrate to the purple color.

SHAPE OF TUBER

Potato tubers vary in shape from a length six times the median diameter to a length about the same as the median diameter. The varieties, the length of whose tubers is not over one and one-quarter times the medium diameter, I have called round. Two selfed round varieties gave only round progeny. Twelve varieties with oval tubers when selfed gave elongated, oval and round progeny. The ratio of other types to round was about nine to one. Either there is a series of factors for shape with the round type as the final subtraction form, or the oval types are heterozygotes of elongated and round. The latter interpretation is more likely to be correct, because oval types have been the popular market types for many years and therefore been used as parents in crosses.

Depth of Eyes

Shallow buds or eyes are required for profitable commercial varieties, yet from one fifteenth to one fourth of the progeny of ten selfed varieties were deep-eyed forms. Three selfed varieties gave no deep-eyed progeny. No progeny of deep-eyed seedlings were obtained, but it seems probable that this character is recessive to shallow eye.

The writer is fully aware that these few observations do not prove that the characters in which potato varieties differ all segregate in Mendelian proportions after crossing. A long series of crosses is necessary to analyze correctly the behavior in inheritance of such characters as shape. On the other hand, the color characters in stem, blossom and tuber are definite and discontinuous, and are alternative in inheritance. The chaotic appearance of the progeny of our commercial potatoes is only apparent. They readily fall into a simple classification and their exact behavior in inheritance could be readily determined if it were not for the difficulties attending successful crossing.

As the writer has previously stated,[3] certain characters pair with their own absence in crossing and these character pairs are the ones affected when a somatic mutation or bud variation occurs in asexual reproduction. Simple loss of the factor takes place. Segregation, therefore, takes place at other times than the reduction of the chromosomes.

---

[3] "The Transmission of Variations in the Potato in Asexual Reproduction," Biennial Report, Conn Agr. Exp. Sta. 1909–1910, 119–161, 1910.

In a previous paper,[4] the writer analyzed the data then extant concerning the hypothesis of degeneration or "running out" of potato varieties. The conclusion was that no degeneration due to continued asexual propagation occurs. No data have been obtained which refute this view, but the study of progeny of selfed potato varieties has suggested an explanation of a certain amount of diminution in yield after long-continued asexual propagation. All commercial potato varieties which have been selfed and their progeny grown, have proved to be heterozygous in at least two characters. It has been shown[5] that when maize biotypes are crossed, the F_1 generation has greater vigor and gives larger yields than the parents. It is a condition apart from inheritance, and is probably due to the heterozygous condition of certain characters in the germ cells. It may be correlated with the actual mechanical operation of segregation. Since potato varieties are retained in cultivation on the basis of yield and since those on the market have been found to be heterozygous in many of their characters, probably the same phenomenon is the cause. May there not be a gradual loss of the stimulus due to crossing through continued bud propagation, so that the variety has only the vigor of one homozygous in the same characters? The variety of course remains heterozygous for those characters in which it was originally heterozygous, yet there may be a gradual decline of the stimulus to cell division than it once possessed.

---

[4] A "Study of the Factors influencing the Improvement of the Potato," Bull. Ill. Agr. Exp. Sta., No. 127, 375–456, 1908.

[5] East, E. M., "The Distinction between Development and Heredity in Inbreeding," AMER. NAT., 43: 173–181, 1909.

SHORTER ARTICLES AND CORRESPONDENCE

THE AGE OF SPEED SIRES

In the May number of the Naturalist, Mr. Redfield makes reply to the criticism of his theory which I made in the issue of January of last year.

Recalling the interest evidenced by biologists when Mr. Redfield's theory appeared some years ago, and considering that no one else has criticized his figures, I assume the question to still be a proper one for discussion.

Mr. Redfield's conception of acquired dynamic development and the data he presented to show its inheritance, strongly suggests the direct transmission of effects of use of the organs.

It is true that more than a majority of successful breeders of trotting horses believe the results of use to be transmitted. A settlement of the question is of no direct interest to horse breeding interests. A change of opinion would not change their practise. Selection and environment are the fundamental factors upon which their work is based. It is immaterial whether they consider one or the other to be of greatest moment; both are imperative. Mr. Redfield would say that the effect of the environment is transmitted. Selectionists would say that the racing test as a feature of environment is an indispensable aid to selection of good individuals and is the only real proof of individual merit.

The fact that a few breeders who regard training as an aid to selection have been as successful as any of the breeders who think otherwise, goes to show that in the breeding of trotters, practises of best breeders vary but little. They differ in their explanation of how the two factors exert their influence upon the results. This lack of agreement, while of no immediate import in practical breeding, because it bears upon a principle involved is of primary interest in the scientific study of heredity.

In my contribution last year, I criticized Mr. Redfield's figures only as they related to the age of sires. He assumes dynamic development to be proportionate to the amount of racing and to the age.

Mr. Redfield's own words will explain the evidence from which he argues for the value of age:

> I said that I took one thousand registered stallions, alphabetically, from the "Index Digest" of the "Register," and calculated the ages of their sires at the time when these registered stallions were foaled. From these I determined that the average time between generations in the male line was 10.43 years, which would give the average age of sires as 9.43 years at the time of service. I then said that, making all reasonable allowances for errors, the average time between generations in the male line might be set down as between 10 and 11 years, and that this period might be used as a standard in testing the age part of the theory. So far no one claims to have tested the accuracy of my calculation; no one claims that the figures I gave were wrong; and no one has said that these figures can not properly be used as a standard; yet if I am to be controverted, one of the first things to be done is to dispute the accuracy of my standard.
>
> I then took the entire list of 2.10 trotters as an appropriate class of animals to be used in testing the inheritance of dynamic development, and I calculated the ages of their male progenitors for four generations. The number of animals involved was over five thousand and I gave the average time between generations in the male line for the production of 2.10 trotters as being approximately 14.00 years. This is an average of nearly 40 per cent. over the standard average determined from the "Register," and my explanation of this remarkable difference was that it indicated the inheritance of acquired dynamic development. So far no one has disputed the accuracy of my computation and no one has attempted to give any other explanation of such an unusual divergence from the natural order of things.

My objection was to comparing the average age of immediate sires in one case with that of all sires in four generations in the other case. I showed that when we take only immediate sires in both cases, it is shown that the average age of the sires of 2.10 horses is practically the same as that of average horses as given by Mr. Redfield.

He now shows that in the case of the 2.10 trotters, while their sires were of an average age of 10.4 years, their grandsires averaged 12.5 years, the great-grandsires 13.5 years, the great-great-grandsires 14.5 years; the stallions appearing in the next two lines at the ages of 15 and 15.98 years.

The evident conclusion from this statement is that our best horses have come from an increasing popularity of *younger* sires.

But this statement regarding the age of sires in various lines is used in contrast with conditions in average horses and the actual figures for the ages of progenitors of average horses are not given to us, but assumed to be much lower. This assumption is erroneous.

It would be very interesting to have the average ages of grandsires, great-grandsires, etc., of the first thousand horses named in the "Index Digest" and used by Mr. Redfield to represent average horses.

I have considered it fairer, however, to use a group, though smaller, more nearly contemporaneous with the 242 horses of 2.10 records used in my previous study. It would be desirable to have a figure based upon the study of the 2.10 list as it stood at the end of 1909, but a comparison of the two groups here used is, I think, a fair one. The group used to represent average horses and as having been bred at about the same time as the 242[1] horses with 2.10 records consists of the first 242 horses registered in Volume 15 of the "Register."

The following tabulation will show that the two groups were contemporaneous:

	Foaled before 1880.	Foaled 1880–1885.	Foaled 1886–1890.	Foaled 1891–1895.	Foaled 1896–1900.
2.10 horses	2	12	40	95	81
Average horses from Vol. 15	2	3	14	116	107

The average age of stallions appearing in each line of the pedigree of the above is as follows:

AVERAGE AGE OF

	Sires.	Grandsires.	Great Grandsires.	Great Great Grandsires.
2.10 horses	9.4[2]	11.5[2]	12.5[2]	13.5[2]
Average horses from Vol. 15	8.28	10.65	11.64	12.78

I am still of the opinion that an impartial study of the figures does not show that age is, of itself, any factor in the inheritance of speed.

F. R. MARSHALL.

OHIO STATE UNIVERSITY.

---

[1] Vol. 22 of the "Year Book" gives 279 fast (2.10) horses, but it is possible to determine the age of the sires of only 242 of these.

[2] One year less than given by Mr. Redfield to show the age of stallionr at the time the foals were sired.

NOTES AND LITERATURE

RUSSO ON SEX-DETERMINATION AND ARTIFICIAL MODIFICATION OF THE MENDELIAN RATIOS

In the April number of the Naturalist Professor Jordan presents an interesting review of recent literature on sex-determination in the course of which he gives an extended account of Russo's[1] experiments with lecithin-fed rabbits. Great importance is attached to this work because it points to conclusions diametrically opposed to those reached within the last ten years by nearly every one else who has studied sex-determination either from the standpoint of the cytologist or from that of the experimental breeder. The nearly unanimous verdict has been that sex-determination is a matter of gametic differentiation, and that the sex of a developing organism is not influenced by conditions of nutrition either applied to it directly or brought to bear upon the mother. The only exception, apparent but not real, as I pointed out in 1903,[2] is afforded by organisms in which both parthenogenesis and sexual reproduction occur. Abundant nutrition favors parthenogenesis, scanty nutrition causes a return to sexual reproduction, including the production of males. Russo has revived the older idea that in non-parthenogenetic organisms also scanty nutrition is a cause of male-production. If true, this is a matter of the greatest importance, both theoretical and practical. Jordan is quite right in so regarding it, but has apparently failed to appreciate the uncritical character of Russo's evidence. This has, however, already been pointed out by several writers, most recently by Punnett,[3] whose brief but convincing paper seems not to have been seen by Jordan. Russo himself has never published the results of his experiments as a whole, but only of *selected experiments* the results of which were favorable to his thesis. This fact alone would throw Russo's claim out of an impartial court, but to be more than fair to Russo, it may be said that his experiments have been repeated twice independently, by Basile[4] and by Punnett, both times with negative results.

---

[1] Russo, A., "Studien über die Bestimmung des weiblichen Geschlechtes," G. Fischer, Jena, 1909.

[2] Castle, W. E., *Bull. Mus. Comp. Zool.*

[3] Punnett, R. C., *Proc. Cambridge Phil. Soc.*, Vol. 15, Pt. 2, p. 92, 1909.

Russo's original evidence consisted of 100 *selected* litters of young borne by lecithin-treated does which included 217 male and 431 female rabbits, and of 100 control litters (likewise *selected*) from non-treated does which included 400 male and 287 female rabbits. The claim is made that lecithin treatment raised the percentage of female offspring from 41.8 to 56.5. Russo in this case proves too much, for his selected controls fall as much below the normal percentage of females as his selected lecithin-treated cases exceed it and, it is fair to assume, for the same reason, because they are *selected.* It is astonishing that a scientist should present such evidence. A prosecuting attorney who should be allowed to decide what evidence should be presented to the court, both for and against, and that all else should be excluded might convict any one of us of all the crimes enumerated in the criminal code.

On the other hand, Basile and Punnett give *all* their results, not selected ones; they mean to tell the *whole* truth, not selected truth. Basile obtained from lecithin-treated does 66 male and 51 female young, or 43.6 per cent. females, while from controls he obtained 225 male and 215 female young, or 48.8 per cent. females. This result is contrary in nature to that of Russo. If any effect is to be ascribed to the lecithin, it is in this case male-production rather than female-production as claimed by Russo. Punnett in repeating Russo's experiments followed methods outlined for him in detail by Russo. They are therefore particularly satisfactory. From lecithin-fed does he obtained 24 male and 23 female young, or 48.9 per cent. females; from controls 54 male and 49 female young, or 47.6 per cent. females. These proportions agree closely with those obtained by Basile, and accord with Hurst's extensive observations cited by Bateson[5] to the effect that "under normal conditions male and female birth are sensibly equal," in the case of rabbits. Finally Heape[6] has criticized on cytological grounds the supposed histological distinction between male and female ova of the rabbit as described by Russo. Heape shows that in all probability the fat-containing, supposedly female ova are degenerating ova.

---

[4] Basile, C., *Atti Acad. Lincei*, Vol. 17, p. 643, 1908.

[5] Bateson, W., "Mendel's Principles of Heredity," 1909.

[6] Heape, W., *Proc. Cambridge Phil. Soc.*, Vol. 14, p. 609.

If further evidence were wanting of the wholly uncritical character of Russo's work, it might be found in his analysis of the results of crosses involving Mendelian color characters. Jordan correctly states Russo's claim, though not his evidence. The claim is that when albino or spotted females were mated with gray or black males, the color character of the latter dominated in the young, but when the same females were first treated with lecithin and then mated with a black male the color character of the mother occurred in part or all of the young. The conclusion is drawn that lecithin treatment of the mother is a practical means of fixing a desired maternal character as a racial character, a claim so astonishing and so important, if true, that with Jordan's indorsement it is in danger of being taken seriously by readers of the NATURALIST. For that reason I have been prompted to examine Russo's evidence carefully and to write this note. His evidence consists of four cases, *all* the cases bearing on this point concerning which he gives detailed information, and he states that these are his *best* cases.

Case 1.—A young albino (Polish) female was treated with lecithin and mated with a gray male and produced two gray young. The lecithin treatment was continued and she was now mated with a black male and had eight young, six white and two black. The reader is led to conclude that the *further* lecithin treatment is responsible for the appearance of white young in the second litter. But is it? No evidence is given as to the gametic character of the male parent of either litter. If the gray male was homozygous he should have produced, as observed, only gray young, though the production of two young only was no adequate test of his character. The *same* male should have been used after the "further" lecithin treatment if information were desired about the effect of lecithin, but this was not done. A new untried male of a different color, black, was used. He produced both albino and black young, a result which indicates that he was heterozygous. If so, the result obtained is such as would have followed without any lecithin treatment whatever! The case proves absolutely nothing, because neither colored parent was tested, so far as we have any information. Russo seems to think that the first litter affords a criterion of what the second should give by a different male parent, a conclusion which no one familiar with Mendelian principles would entertain for a moment.

Case 2.—A young Himalayan (albino) female rabbit was treated with lecithin and mated with a black male. She produced by him three litters of young. The first litter contained six young, all black. The second litter contained four young, two of which were Himalayan, two yellow-and-white.[7] The third litter contained seven young, concerning the color of one of which no account is given; four were Himalayan, one yellow-and-white and one black-and-white. The case (a selected one) is supposed to show that continued treatment with lecithin produces more young of the maternal type in later than in earlier litters. But a *selected case* can not fairly be used to show anything of the sort. Only a fairly uniform result of repeated experiments could establish it. Under the circumstances we can only ask what the expected Mendelian result would be in a case like this if no lecithin treatment were involved, and then inquire whether the observed result differs in any respect from it.

If no lecithin treatment were involved we should say that the black male used was heterozygous in the recessive characters albinism, spotting and yellow; and the expectation would be that he would produce young of five sorts in one of the following distributions, depending on the gametic character of his albino mate:

Black		**Yellow**		**Black and white**		**Yellow and white**		**Albino**
1	:	1	:	1	:	1	:	4
3	:	3	:	1	:	1	:	8
9	:	3	:	3	:	1	:	16

The observed distribution for the three litters is 6 : 0 : 1 : 3 : 6. This is so good a Mendelian result that it would not call for any special comment in ordinary breeding work. Further matings would be called for, but it would be surprising if these did not supply the missing class, yellow, and give numbers agreeing more closely with one or another of the suggested ratios.

No control matings of either parent in case 2 are recorded by Russo.

---

[7] Regarding this class Russo says they were of the same race, as the mother but with yellowish or white ground-color ("von derselben Rasse, aber mit gelblicher bzw. weisser (wie in Fig. 27), Grundfarbe"). But the photograph, Fig. 27, shows unmistakably that these animals were not albinos at all but Dutch-marked colored animals, which invariably have dark eyes. A spotted dark-eyed animal is not by any means of the "same race" as an albino, as is well known to students of genetics. Spotting behaves as a Mendelian unit-character wholly independent of albinism.

Case 3.—The statements of Russo concerning this case are very incomplete. A spotted "Olandese" female after lecithin treatment was mated with a silver-gray male and produced three spotted and one self-colored young, which are figured. Before treatment with lecithin she had been mated under normal conditions (*once* with the same silver-gray male, "mit demselben grau Männchen einmal," but we are not told that he was the father of the young, we are rather left to infer that she may have mated with other males also. Five young were afterward born—"es erzeugte dann später 5 Junge," all gray. Again the female was mated under similar uncertain conditions, "unter den gleichen Bedingungen," and produced four gray young. Since in a third litter, after lecithin treatment, she produced spotted young, it is concluded by Russo that the lecithin treatment was responsible for the changed result. But before accepting this conclusion we should like to be assured that one and the same male was used in both cases. The silver male may have been heterozygous in spotting, the father of the earlier litters not.

Case 4.—Two Himalayan (albino) females, sisters, were mated with the same black male. One of the two was lecithin treated, the other was not. Both produced black young, five each. This looks like a bad case to select in support of lecithin influence, but we are told further that in the following year, when lecithin injections were employed forty days previous to copulation, a litter of two Himalayan young was obtained. The sire of the litter is figured but we are not told whether he was the *same* as the one used the previous season. This omission is significant. The male figured was evidently heterozygous in albinism, but it is a pretty safe guess that he was not identical with the male used the previous season, which was in all probability homozygous in black. In this case as in the others described by Russo it is impossible to avoid the impression that the author is not making a full and frank statement of facts but is stating half-truths likely to mislead the unwary. In Jordan's case this is exactly what has happened. He says: "The evidence here appears unequivocal that external conditions (*e. g.*, nutrition) can determine the kind of sex *and entirely vitiate the Mendelian scheme of ordinary crosses*" [italics mine]. I have, however, presented in detail *all the evidence* which Russo gives in support of the assumed vitiation of Mendelian inheritance. I think the reader will agree with me that the evidence is more than equivocal and that the vitiation is of reasoning not of inheritance.

So far as I know, only one other investigator besides Russo has laid claim to having modified the ordinary course of Mendelian inheritance by external conditions. Such a claim, if I rightly understood him, was made by Professor W. L. Tower, in a paper read at the last annual meeting of the American Society of Naturalists, in the case of beetles of the genus Leptinotarsa. Detailed information regarding the cases in question will be awaited with much interest. It is to be hoped that this will prove more complete and satisfactory than Russo's.

W. E. CASTLE.

HARVARD UNIVERSITY,
June 11, 1910.

THE BUBONIC PLAGUE

BUBONIC plague is primarily an animal disease. Its original victim is said to have been a species of rodents found in the mountains of Mongolia. Several Russian scientists have sought to establish this hypothesis, according to which the *Arctomys bobac*, a Mongolian marmot, is the primitive animal host. In it the disease is permanently prevalent, and from it both man and the rat are infected periodically. According to the view of these writers the final eradication of the plague from our globe would be accomplished by the extermination of this rodent. That this view is over-optimistic may be inferred from the probable existence of other ancient centers from which plague epidemics have originated, and in which, consequently, permanently infected animals are at home, and also from the recent origin of such an established center of animal infection on our own continent.

In the introduction to an article on Plague Eradication Measures (Squirrel Campaign) in California, Rucker[1] comments on the epizootic which for four years has been spreading among the ground squirrels of Contra Costa County, and which more recently has been reported from other districts also. The animal infected is *Citellus beecheyi*, which is reported by ranchers to have died by the thousands in 1904–5–6. In appearance and habits, it resembles closely the Thibetan marmot referred to above. Not until there came cases of human plague due to plague-infected squirrels was the disease of the latter subject to careful scrutiny. Wherry[2] first showed in a conclusive manner that ground squirrels, obtained from two widely separated sections of California, were infected with the bacillus of bubonic plague. There remained to be ascertained the extent of the infection and appropriate methods for the extermination of the infected animals and the eradication of the disease, which had gained apparently a permanent foothold on the state of California. The records of these investigations form one of the most interesting and important chapters of medical zoology yet written.

---

[1] *Journal Amer. Med. Assn.*, Vol. 53, p. 1995.

The splendid work which has been done by the Public Health and Marine Hospital Service on the Pacific coast in connection with the problem of stamping out bubonic plague, has included investigations on the rats and also on native rodents, which have established important points in the relations of these animals to the spread of that disease. While no cases of human plague have been reported for many months, yet plague-infected rodents have been killed at one point or another as recently as February. The disease is not common, since about 2,000 squirrels from one county were examined before an infected individual was found. Nevertheless, one can not doubt its continuance among the wild rodents, or question the advisability of prosecuting the campaign for the total eradication of the infected animals. The service has published[3] complete statistics of work to date and a map showing the area studied and the prevalence of plague among ground squirrels.

The rodents in which plague infection has been demonstrated include both the introduced species, *Mus rattus,* the black rat, and *Mus norvegicus,* the brown rat, and also the native species, *Citellus beecheyi,* the California ground squirrel, and *Neotoma fuscipes,* the brush rat. The work of McCoy[4] corroborated fully the findings of Wherry, and left no doubt that the disease among ground squirrels is due to the same organism that causes bubonic plague among rats and men. The experimental evidence which the latter reports in a conservative and critical manner includes several typical cases of plague in human beings where the diagnosis has been verified by bacteriological methods, and where the cases "have been traced to squirrel infection as clearly as one can trace such things." While McCoy states that in his opinion the number of human beings infected directly by squirrels will never constitute a large element in the infected region, yet, on the other hand, one can not deny the patent facts that the infection of native rodents provides a retreat in which the disease is relatively safe from elimination and also a source from which it may be at any time transmitted anew to the human species. The transmission from rat to man through the intermediation of the fleas is easily conceived. The intimate association of the rat with human dwellings and with places constantly visited by man makes the transfer of the infected fleas an easy matter. The transmission of the disease in similar fashion among the animals in a squirrel colony is equally readily understood, though the booby owl, which regularly occupies the same burrows with the ground squirrel, may play the important part in the dissemination of the disease, since the bird, flying from burrow to burrow, might readily carry infected fleas over long distances. If this be true, the eradication of the disease is greatly complicated.[5] The intimate association of rats and ground squirrels has been observed repeatedly. In one locality in the outskirts of a city both were taken alive from the same burrows and rat fleas were combed from the hair of the squirrel.[6]

---

[2] *Journal of Infectious Diseases,* Vol. 5, p. 485.

[3] "Public Health Reports," Vol. 25, p. 585.

[4] "Public Health Reports," Vol. 25, pp. 27–33.

The mode of transfer from squirrel to man is more difficult to understand. Simpson[7] suggests that cattle on the range are the unrecognized factor which provides for the conveyance of infected fleas from squirrel to man. He states that fleas abound in and about squirrel villages and the cattle as they range over this territory lie down to rest in and among these villages. Since the fleas quickly desert an animal after death, the cattle will more readily acquire fleas in villages containing infected squirrels, and especially if dairy cattle were concerned, the daily contact with men would give abundant opportunity for the transfer of the infected fleas. Some of the squirrel villages known to be plague infected are so isolated as to afford only occasional contact with man, yet cattle were seen grazing near these villages and may furnish the connecting link in transmission.

Of the species of wild rodents known to be infected in nature, the California ground squirrel, *Citellus beechyi*, is unquestionably the most important. It has also been the longest recognized as an element in the plague situation. Its habits and distribution have been outlined by Merriam,[8] who also discusses means for its systematic destruction.

---

[5] Rucker, W. C., "Public Health Reports," Vol. 24, p. 1225.

[6] "Public Health Reports," Vol. 25, p. 623.

[7] "Public Health Reports," Vol. 25, p. 250.

Much less well known is another California rodent which has very recently been shown to be susceptible to bubonic plague under natural conditions. This species is the woodrat, *Neotoma fuscipes annectens* Eliot. It is distinctly a new world form, of which several species occur on the Pacific coast and into the desert region as far as Utah and Colorado. Evidently, if the infection can be transmitted from one to another of these species, the disease will thus extend over a large area. Rucker,[9] says of their habits:

> Wood rats are nocturnal in their habits and are seldom seen in the light of open day except when it is very cloudy. For the most part, they are found along small wooded arroyos, in which they build their nests, often of the most elaborate design. Those which the writer has had the opportunity of dissecting consist of pieces of driftwood arranged in a pile, sometimes 6 or 7 feet in diameter and 3 feet high. There is usually only one entrance to the nest and this is lined with sharp sticks. It is said that where cactus is plentiful the tunnel is lined with cactus spines as a protective measure against other mammals. The interior of the nest is frequently arranged into three stories, and contains storehouses and living rooms. Usually there is an exit which is frequently found near the base of a tree. This is utilized as a means of escape when the ordinary entrance is blocked and some enemy begins to tear the nest apart. The storehouses in several instances contained large quantities of the corms of a plant growing in the immediate neighborhood. Although wheat was growing but a few hundred yards away, none of this was found in these nests. In certain regions the *Neotoma* store up large quantities of mesquite beans, and these caches are raided annually by the Indians, who use them for food. They also store up mushrooms, certain varieties of puffballs and acorns.

In view of the part played by fleas in the transmission of the disease, it is interesting to note the average number of fleas from a squirrel is much larger than from a rat or from any other host yet observed. Much collateral work has been done on the species of fleas, found on the various rodents which suffer from bubonic plague, and on the relations of these fleas to the transfer of the disease as shown by their ability or readiness to bite man and other hosts. The majority of the two rat fleas common in San Francisco, viz., *Lœmopsylla cheopis* Roth and *Ceratophyllus*

---

[8] "Public Health Reports," Vol. 23, No. 52.

[9] "Public Health Reports," Vol. 25, No. 1, p. 2.

fasciatus Bosc., will bite man under experimental conditions, while the squirrel fleas, *Hoplopsyllus anomalus* and *Ceratophyllus acutus*, feed readily on man's blood.[10] The same authors have also shown[11] that fleas from rodents will adapt themselves to a host of a different species and that fleas from squirrels will attack rats even in the presence of their normal host. Plague bacilli have been demonstrated in both the common squirrel flea, *Ceratophyllus acutus*, and also in the lice (probably *Hæmatopinus montanus*) very commonly found on the same host.[12] Experimental work has also been done to determine the susceptibility to bubonic plague of other rodents in which the disease has not yet been reported under natural conditions.[13] Finally in experimental cases[14] rat fleas have conveyed plague from rats to ground squirrels and squirrel fleas from squirrel to squirrel, and also to guinea pigs and rats.

H. B. WARD.

DESERT PLANTS[1]

In the opinion of the reviewer, this book constitutes the most noteworthy contribution thus far submitted from the Desert Botanical Laboratory. In a measure it may be said to be the outcome of previous contributions and others not hitherto published. Investigations in progress there during the several years since the establishment of the desert laboratory, while they have a wider range of application, have centered in the effort to describe and interpret the interplay of stimulus and response as between desert environment and plants in the desert. It in no way detracts from the merit of Professor Spalding's contribution to say that the results of these investigations constitute a prominent feature of the book, and indeed it stimulates increased appreciation of his work to observe that he assumed the difficult task of so correlating the results of a staff of specialist investigators as to bring about a reasonable measure of interpretation of the rôle of environmental stimuli in shaping the origin, distribution, associations and movements of desert plants. The book lays claim to being only a partial interpretation of the problems of desert vegetation and expressly points out the need of continued investigation not merely of the area under consideration (the so-called "Desert Laboratory domain"), but of comparative studies of more areas widely distributed through the desert.

---

[10] McCoy and Mitzmain, "Public Health Reports," Vol. 24, No. 8.

[11] "Public Health Reports," Vol. 24, p. 1013.

[12] Geo. W. McCoy, "Public Health Reports," Vol. 24, p. 475.

[13] Geo. W. McCoy, *Jour Infectious Diseases*, Vol. 6, p. 283.

[14] Public Health Reports, Vol. 25, p. 465 and 659.

[1] "Distribution and Movements of Desert Plants," by Volney M. Spalding, Carnegie Institution of Washington, publication No. 113, October, 1909, pp. 144, with 30 plates.

Having set itself the task of interpreting the ways of plants in the desert, the management of the desert laboratory began by investigating intensively a small area of typical desert country. The laboratory site appears to have been selected with a view to having at its door this ideal field of investigation, which is an area of not over a mile in radius.

Professor Spalding rightly supposes that no other small area anywhere has had centered upon it the intensive study of so many well-equipped investigators as has this typical bit of desert, and he might have added that perhaps in no other case has there been a more adequate equipment of apparatus and instruments for work of a precise nature and, in the reviewer's opinion, no other instance where more adequate methods have been devised for pursuing the investigations.

The work of collaborating specialists is largely presented as distinct sections or chapters of the book.

The geology of the vicinity of the Tumamoc Hills is presented with particular reference to its relation to the distribution and movements of plants by Professor C. F. Tolman, of the University of Arizona (pp. 67–82), in the chapter on Environmental and Historical Factors. In this chapter also Dr. B. E. Livingston contributes a section (pp. 83–93) on the soils of the desert laboratory domain. Reference is made here likewise to the evaporation studies conducted by Dr. Livingston. It is of course beyond the range of the present reviewer's task to take up Dr. Livingston's work in detail, but it seems an appropriate place in which to point out a striking case in which endowed research has yielded results of far-reaching application in behalf of economic development, namely, in the relation of soils and evaporation to plant production generally.

Dr. W. A. Cannon, of the Desert Laboratory staff, contributes a thoroughgoing study of the root system of the giant cactus (*Cereus giganteus*), together with a comparison of the root systems of certain other marked desert species (pp. 59–66). Such specific studies furnish the source of reliable data for conclusions as to the relation which the habits and structure of plants bear to their distribution.

Floristic investigations have been undertaken by Professor J. J. Thornbur, botanist of the Arizona Experiment Station, and reported in an effective manner under the title Vegetation Groups of the Desert Laboratory Domain (Chap. IV, pp. 103–112). In this contribution, floristic studies, instead of being dry lists of species, are made to contribute materially to the chief questions as to the origin, association and movements of the vegetation.

In the chapter devoted to defining plant associations and habitats, pages 24 to 27 embrace an account of the lichens of the Laboratory domain, by Professor Bruce Fink, of Miami University.

Distributional maps with accompanying notes were prepared by Mr. J. C. Blumer, of the laboratory staff. In the reviewer's opinion maps of this sort, showing, as they do, location and individual frequence of notable species, are of essential help to the reader, as they must have been indispensable to the writer of the book.

Finally, among the collaborative contributions is a chapter (V, pp. 113–119) on the Origin of Desert Floras, by Dr. D. T. MacDougal, director of the Desert Laboratory and of the Division of Botanical Research of the Carnegie Institution of Washington.

In this study of the vegetation of the Desert Laboratory domain Professor Spalding has led the attack from the plant side, seeking to define the actual conditions of distribution, association and movements in the vegetation as a whole and specifically in the case of prominent desert species, and always with a view to relating facts of distribution, structure, etc., with the environmental conditions under which they have been worked out.

Accordingly, a considerable portion of the book is of a descriptive nature. Chapter I presents the plant associations and habitats of the laboratory domain. The author distinguishes some twelve associations exclusive of parasitic and symbiotic plants and miscellaneous introduced species, meaning by "association" an aspect or phase of vegetation, such, for example, as the cottonwoods and willows of a river bank, a mesquite forest, or chaparral made up chiefly of palo verde and catclaw or, on the other hand, of Mexican greasewood. These associations reflect topographic and soil conditions of the area. Remembering the traditional view as to the hostility of the desert toward plants, one is rather surprised to learn that this inhospitable domain harbors between four and five hundred species which are by no means all xerophytes, but species adjusted to the most diverse moisture requirements. To be sure, this is due in a measure to the inclusion of a river and its flood plain in the Laboratory domain. Still, a surprising number of species manage to exist on the arid situations without being marked by any special xerophytic structures.

Chapter II takes up in detail an analysis of the distribution of certain of the most prominent desert species. As to the factors determining the local distribution and association of species, these are, just as everywhere else, chiefly topographic and soil conditions. Manifestly it is primarily the water supply as affected by conditions of soil and topography which is the critical factor, but soil drainage or aeration is found to play a large rôle and, indeed, is the determining factor in the distribution of certain species.

Special attention may be called to that portion of Chapter II which presents the facts and conclusions as to aspect preference as exhibited on the laboratory domain. The question, in brief, is to account for the differences in the vegetation covering of slopes having a general southerly exposure as compared with those having a general northerly one. Here is found fully justified the claim advanced by certain American plant ecologists, that only by exact quantitative study of the items involved may one expect to arrive at an explanation of distribution, association and movements of plants. In this connection the study of the root system of *Cereus giganteus* sustains its status as a model piece of ecological investigation.

Another thing which we learn from this chapter (II) is that while, as we supposed, the chief struggle of plants in the desert is against the physical environment, there is still a right marked element of competition amongst desert species with its consequent features of accommodation (commensalism?) or of extermination and succession. Since, however, the problems of distribution, association and movements are so little complicated by the factor of crowding as compared with mesophytic forest societies, for example, it has seemed to the reviewer that the desert furnishes about the simplest as well as the most inviting point of attack for the ecologist.

In chapter VI under Review and Discussion and in Chapter VII, a summary, Professor Spalding brings forward in condensed form a survey of the work of investigation done on the laboratory domain and particularly the tentative or positive conclusions he is able to formulate as a result of these investigations. So far as regards the local distribution and association of species, the reviewer is unable to discern that the general view thus far held as to the rôle of the so-called edaphic factors is in any wise modified, but our knowledge of the manner in which this rôle is played has been materially enriched by the work of Professor Spalding and his collaborators.

Foregoing the temptation to comment on many other interesting details of this book, there remains yet to consider the crowning question as to whence came the desert vegetation and how did it come to be what it is? Upon this point Professor Spalding's conclusions are quite positive, as indicated in the following words from his book:

> The general continuity of geological history since the Tertiary indicates a relatively long period within which plants of the Laboratory domain have one by one or at any rate by no mass movements, become established in their places. There is reason to believe that throughout this period the processes now going on before our eyes have been in progress. The present flora, therefore, may be assumed to be merely the final stage so far of just such a series of events as are now observable. . . . The small area within its limits (the Laboratory domain) has received representatives of genera that have shared in the great migrations south and north along the Cordilleras, but through the time that has elapsed since the greater movements it has also received by entirely ordinary means the plants that have come and are still coming to it.

We are unable to gather from these words whether Professor Spalding means that "the processes going on before our eyes" relates simply to movements of vegetation or includes also modifications whereby ecological types—as, for example, the giant cactus—arise. In this connection, Dr. MacDougal's chapter on the origin of desert floras is illuminating. His view is in agreement with Professor Spalding's as to the fact that there is little evidence of extensive migrations of the characteristic xerophytes of this desert from which it is to be inferred that these investigators believe the Sonoran desert to have been and to be now a center of origins for its flora. MacDougal brings us face to face with the question as to *how the desert makes its flora* if one may give the question this popular cast. He rejects the idea of so-called adaptive changes representing ontogenetic and morphogenetic responses (made by a plant when exposed to desert conditions, for example) as being not necessarily adaptive and in any event not capable of being transmitted to offspring. He believes, however, that what has been observed to take place under experimental conditions might take place when plants or generations of plants are subjected to the stimulus of desert environment. His words are:

> The influence of external conditions upon the germ plasm, however, has been seen to produce irreversible changes in a hereditary line by which new combinations of qualities and new characters were called out, which were fully transmissible. Furthermore the newly produced forms perished in some localities endured by the parental type, but exceeded it in weathering the conditions of other localities.

In the treatment of the larger aspects of the question of the origin and movements of desert plants the intensive study of a single small area fails to furnish a large enough fund of comparative data to make a wholly satisfactory basis for conclusions. The reviewer would modestly suggest that the Sonoran desert (meaning the desert areas of our southwest and of northern Mexico) is a very large and diverse region in which not merely individual species but whole genetic groups have become xerophilized (with apologies for spurious coinage), and that correlated investigations at numerous points and a study of genetic relationships in connection with distribution, association, movements and modification (meaning transmissible qualities or characters) would furnish a broader basis for the interpretation of the ways of plants in the desert at large.

In a final word the reviewer would invite attention to the status of Professor Spalding's book considered in relation to plant ecology. In full appreciation of other recent ecological contributions of similar merit the opinion is advanced that this book stands in a special way as an index of the new era in geographic ecology in which a field of botanical research which was prone to abound in verbosity and in the discovery of "adaptations" has been brought to the status of a more exact science employing quantitative methods of study. It is not boastful to say that this newer phase of plant ecology represents especially the outcome of the teaching and investigations of a small group of American botanists (of which group the present reviewer can not claim to be a member) who have sought to put the study of plant relations upon the same basis as that pursued in the study of plant physiology in the limited sense.

WILLIAM L. BRAY.

BOOKS **WILLIAM J. GERHARD,**

2209 CALLOWHILL STREET, PHILADELPHIA, PA.,

offers the following at affixed net prices. Extended catalogues of books and pamphlets in all branches of natural history post-free on request :

1.	American Journal of Conchology. 7 vols., partly bound	$25.00
2.	American Journal of Science. Second Series, volumes 1–10. Half roan (3 vols. somewhat waterstained)	10.00
3.	American Mineralogical Journal (Bruce). 1 vol., 1814. New half morocco	10.00
4.	American Monthly Microscopical Journal, vols. 1–20 (1888–1899), of which 14 vols. are half roan	15.00
5.	American Naturalist, vols. 1–6 (1868–72)	9.00
6.	Annals N. Y. Academy of Science, vols. 4–14 (1887–1898). Cloth	22.50
7.	Annuaire du Musée Zoologique de l' Académie des Sciences, St. Petersbourg, vols. 1–7 (1896–1902), lacking one number of vol. 1	10.00
8.	Bulletin American Museum of Natural History, vols. 1–11 (1887–1901)	27.50
9.	De Kay. Zoology of New York—Birds. 4to. Cloth. 141 colored plates	10.00
10.	Gaudry, A. Animaux fossiles et géologie de l'Attique. 2 vols., folio, 1862–67. Half calf, 75 plates and map	35.00
11.	Harlan, R. Medical and physical researches, etc. 1835. Cloth	7.50
12.	Journal and Proceedings Royal Society of New South Wales, vols. 11 (1877) to 23 (1890), except vol. 14. Partly bound in cloth	13.00
13.	King, C. United States Geological Exploration of 40th Parallel. Complete set, 7 vols., quarto, cloth, and two folio atlases	22.50
14.	Microscope (The), vols. 4–11. 8 vols. in four. Half roan	7.50
15.	Morton, S. G. Synopsis of the organic remains of the cretaceous group of the United States. 1834. Half roan. Rare	15.00
16.	Pritchard, A. History of Infusoria, including Désmidiaceae and Diatomaceae. Fourth (last) edition. 1861. Half morocco	8.00
17.	Proceedings Lit. and Philos. Society of Liverpool, vols. 1–34 (except vols. 5, 10, 11, 12, 16, 17, 20, 21), partly bound	16.00
18.	Reports of Explorations and Surveys . . . for a railroad from Miss. River to Pacific Ocean. 13 vols. 4to. Bound	12.00
19.	Smithsonian Miscellaneous Collections, vols. 1–6 (1861–67). Scarce	13.50
20.	Sowerly and Lear. Tortoises, terrapins and turtles drawn from life. Small folio, 1872. Half morocco, 60 finely colored plates	11.00
21.	Transactions American Entomological Society, vols. 1–6. Bound. Scarce	35.00
22.	Transactions Geological Society of Pennsylvania. 1 vol. (1835.) All issued. New half morocco. Rare	15.00
23.	Winter, G. Die Pilze Deutschlands, etc., vols. 1 and 2 (1884–87). Half morocco	7.50

Methods in Plant Histology

By CHARLES J. CHAMBERLAIN

Second edition, revised and much enlarged; 272 pages, with 88 illustrations, 8vo, cloth; net $2.25, postpaid $2.39

THE first complete manual to be published on the subject of botanical microtechnique. It contains detailed directions for collecting and preparing plant material for microscopic investigation, setting forth the advantages and disadvantages of the different methods.

Will no doubt find a place in every well-regulated library, and will be found very useful by private students.—*Plant World.*

It is an excellent book for the individual worker and for classes in colleges.—*Education.*

A Laboratory Guide in Bacteriology

By PAUL G. HEINEMANN

158 pages, interleaved, with 37 illustrations, 12mo, cloth; net $1.50, postpaid $1.61

A CLEAR and concise presentation of bacteriological technique, designed principally as a manual for the medical student, but highly useful also as a reference book for the biological teacher and investigator, as well as for practical workers in the fields of medicine and hygiene.

The instruction given is clear and accurate, and the practical exercises are well selected.—*The Lancet* (London).

A book such as this must facilitate very greatly the practical class work, for which it is most excellently adapted. — *American Journal of Medical Sciences.*

The directions are clear and concise, and every stage is described so carefully that it is hard to see how the student can go astray. Physicians who are rusty in bacteriology cannot do better than buy this little book. The book is beautifully printed and bound.—*American Journal of Clinical Medicine.*

Animal Micrology:

Practical Exercises in Microscopical Methods

By MICHAEL F. GUYER

250 pages, 8vo, cloth; net $1.75, postpaid $1.88

THE title of this book will explain its scope. It is intended as a laboratory manual for textbook use. Its aim is to introduce the student to the technique of microscopic anatomy and embryology, emphasizing details of procedure rather than descriptions of reagents or apparatus. Sufficient account of the theoretical side of microscopy is given to enable the student to get satisfactory results from his microscope.

The directions are simple, explicit, and complete.—*American Journal of Clinical Medicine.*

The medical student will find it very useful as a guide to microscopic work.—*Journal of the American Medical Association.*

This is one of the cleanest works on microscopical technique we have ever seen, and is especially suitable for the beginner. It is full of points, tricks of technique not mentioned in other works, and is one that every student and physician should have.—*Medical Century.*

This valuable book is strong through its rigid exclusion of the trite and the conflicting. It is lucid and helpful, because a man long practiced in practical work has given what he believes the most expeditious and reliable method of obtaining a definite and comprehensive result. — *Medical Notes and Queries.*

A concise, eminently practical, and well-classified treatment.—*Science.*

The expositions of the methods recommended are admirably clear.—*Nature.*

One of the best and most practical works upon microscopic technique with which we are acquainted.—*American Naturalist.*

As a textbook it can hardly be improved. The research worker will find in this book just the information he frequently needs in preparing material with which he is not familiar.—*School Review.*

It does present in very clear form a judicious selection of methods, including an excellent untechnical account of the microscope and its optical principles, adequate for the undergraduate course in histology.— *Journal of Comparative Neurology and Psychology.*

ADDRESS DEPT. 64

Chicago **THE UNIVERSITY OF CHICAGO PRESS** **New York**

VOL. XLIV, NO. 524 AUGUST, 1910

THE
AMERICAN
NATURALIST

A MONTHLY JOURNAL
Devoted to the Advancement of the Biological Sciences with
Special Reference to the Factors of Evolution

CONTENTS

Page
I. Chromosomes and Heredity. Professor T. H. MORGAN - - - - - 449
II. Spiegler's "White Melanin" as related to Dominant or Recessive White. DR. ROSS AIKEN GORTNER - - - - - - - - 497
III. Shorter Articles and Correspondence: A Pickwickian Contribution to Our Knowledge of Wasps: Professor KARL PEARSON - - - - - - 503
IV. Notes and Literature: Heredity, DR. W. J. SPILLMAN - - - - - 504

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

TO ORNITHOLOGISTS AND MUSEUMS

W. F. H. ROSENBERG

Importer of Exotic Zoological Specimens

57 Haverstock Hill, N.W., England

Begs to announce the publication of a new Price List (No. 11) of Bird Skins. This catalogue contains over 5,000 species, and is the largest and most complete price list of birds ever published. It is arranged in systematic order, based on the classification of the British Museum "Catalogue of Birds," with authors' names, indications of localities, and an index to families. It will be sent gratis and post free on application, as will the following lists:

No. 7, Mammals; No. 8, Birds' Eggs;
No. 9, Reptiles, Amphibia, and Fishes.

Largest stock in the world of specimens in all branches of Zoology.

Specimens sent on approval.

Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

Henry Holt & Company

34 West 33d St., New York
378 Wabash Ave., Chicago

Microscopes and Accessories

Hand Cameras of Highest

Binoculars, Prism and Galilean

the best obtainable for Nature Study

Scientific Instruments

Laboratory Apparatus

Max Meyer 18 West 27th St. New York

"Quality, Prices, Service Right."

THE
AMERICAN NATURALIST

VOL. XLIV August, 1910 No. 524

CHROMOSOMES AND HEREDITY

PROFESSOR T. H. MORGAN

COLUMBIA UNIVERSITY

THE INDIVIDUALITY OF THE CHROMOSOMES

WE have come to look upon the problem of heredity as identical with the problem of development. The word heredity stands for those properties of the germ-cells that find their expression in the developing and developed organism. When we speak of the transmission of characters from parent to offspring, we are speaking metaphorically; for we now realize that it is not characters that are transmitted to the child from the body of the parent, but that the parent carries over the material common to both parent and offspring. This point of view is so generally accepted to-day that I hesitate to restate it. It will serve at least to show that in what I am about to say regarding heredity and the germ-cells I shall ignore entirely the possibility that characters first acquired by the body are transmitted to the germ. Were there sufficient evidence to establish this view, our problem would be affected in so far as that we should not only have to account for the way in which the fertilized egg produces the characters of the adult, but also for the way in which the characters of the adult modify the germ-cells.

The modern literature of development and heredity is permeated through and through by two contending or contrasting views as to how the germ produces the characters of the individual. One school looks upon the egg and sperm as containing *samples* or *particles* of all the characters of the species, race, line, or even of the individual. This view I shall speak of as the *particulate theory of development.*

The other school interprets the egg or sperm as a kind of material capable of progressing in definite ways as it passes through a series of stages that we call its development. I shall call this view the *theory of physico-chemical reaction,* or briefly the reaction theory. The resemblance of this comparison to the traditional theories of præformation and epigenesis is obvious, and I should willingly make the substitution of terms were it not that the terms præformation and epigenesis have certain historical implications, and, as I wish to emphasize certain things not necessarily implied in the historical usage, I prefer descriptive terms other than these overladen with so many traditions.

A few preliminary considerations will serve to clear the way for the detailed examination to follow:

The particulate theory may appear more tangible, definite and concrete because it seems to make a more direct appeal to a material basis of development and heredity. The theory of physico-chemical reaction may seem more vague and elusive, since the responses and reactions to which it must appeal are as yet little known. But this distinction is not one of much importance. For the particulate theory requires as elaborate a series of processes or changes to account for the distribution of the postulated particles and their development into characters as does the reaction theory itself, and on the other hand the reaction theory may rest its claims on as definite a physical or material basis as does the other view. One theory lays emphasis on the material particles of development, the other on the changes or activities in the same material. Both views assume that there is something in the egg that is responsible for every detail of character that later develops out of the egg. Since we do not know what this something is, it must be admitted at the outset that the distinction between the two is largely theoretical and possibly temperamental. To some minds it appears that to admit that every detail of character is represented by the egg must mean that something material in the sense of some actual particle that stands for each detail must be present. To other minds it seems only necessary to admit that eggs are made of different materials in order that the outcome of the development may be different, and that these differences between eggs, while leading to differences in the end product, need not be conceived as different material particles in the sense that the particles become the ultimate characters that differ.

Both views postulate an initial difference in the egg, but one view conceives the differences in the egg to be associated with particles that are in some way directly responsible for the different characters, while the other view conceives adult characters to be the product of an elaborate series of processes and that the material differences in different eggs are too remotely connected with the end product of their development for us to think of those differences in terms of special or separate particles except in the purest symbolic fashion. Whichever view we adopt will depend first upon which conception seems more likely to open up further lines of profitable investigation, and second which conception seems better in accord with the body of evidence at hand concerning the process of development.

It may be said in general that the particulate theory is the more picturesque or artistic conception of the developmental process. As a theory it has in the past dealt largely in symbolism and is inclined to make hard and fast distinctions. It seems to better satisfy a class or type of mind that asks for a finalistic solution, even though the solution be purely formal. But the very intellectual security that follows in the train of such theories seems to me less stimulating for further research than does the restlessness of spirit that is associated with the alternative conception. The purely adventurous character of any explanation offered by the reaction theory seems more in accord with the modern spirit of scientific theory. But when we lay aside these generalities concerning the two theories and descend to particulars we may find at times very real distinctions between the two views. For example:—

The original conception of præformation postulated an actual material embryo in the egg; epigenesis denied the existence of that embryo, and justified its denial. Here surely there was a real distinction.

But the problem has refined itself in modern times. We no longer look for an actual embryo præformed but we look for samples of each part, which samples by increasing in size and joining suitably to other parts make the embryo. This is modern præformation. Is it not a question of fact whether such samples exist in the egg? The contrasting theory looks upon the germ-cells as consisting of one fundamental material, or at most of a few materials that change as development proceeds, until finally the end-product of the changes are the kinds of materials that we know to differ chemically in a number of ways. It seems to me that there is here also a real difference between the two views, and that the one can be as clearly formulated as the other: I propose, therefore, to examine further these contrasting views in the light of our present opinions concerning the egg and its mode of development.

The *modern* theory of particulate inheritance goes back no further than the discovery that the sperm transmits equally with the egg the characters of the race; and with the discovery that the most conspicuous thing that the sperm brings into the egg is the nucleus of the male cell or more specifically its chromatin. Around these simple statements the whole edifice has been erected. We owe to Weismann more than to any other biologist, the peculiar trend that this speculation has followed. It has seemed to many biologists that the only interpretation of the facts just stated could be that special turn that Weismann has given to them.

By a curious twist of logic Roux brought the chromosomes into the discussion. He argued that the karyokinetic figure is an instrument of such a sort that we must suppose its function to be that of nicely separating at each division the different kinds of materials of which the chromosomes are composed, or supposed to be composed. Were it only necessary, he argued, to divide the chromatin quantitatively into equal parts a far simpler mechanism ought to suffice. Weismann took this argument in good faith, and built up his theory upon it.

But if one thing seems more certain than anything else in modern cytological work it is that in most cases the karyokinetic figure divides the chromatin of the chromosomes into exactly equal parts, irrespective of what the fate of the cells is to be. We find that the chromosomes in the different tissues are identical as far as our methods reach. Observation gives a positive denial to the Roux-Wiesmann assumption. In fact, Roux himself has later abandoned this position. We find in many quarters a strong disinclination to the view that the chromosomes are responsible *in this sense* for the process of development.

This feeling has interested me a good deal in recent years, especially since I myself have felt the same disinclination to reduce the problem of development to the action of specific particles in the chromosomes. In my own case and possibly in the minds of others this hesitation is due in the first place to a distaste for the particular form of this theory that Weismann has made so pronounced a feature of his speculations, and in the second place to a feeling that it is unsafe or unwise to reduce the problem of heredity and development to a single element in the cell; when we have every evidence that in embryonic development the responsive action of the cytoplasm is the real seat of the changes going on at this time, while the chromosomes remain apparently constant throughout the process.

The feeling against the view that ascribes everything to the chromosomes has been increased also by the assumption that unit characters in heredity are præformed; especially since those who assume such characters to be the basis of heredity have as a class—with some exceptions, however—shown a strong predilection towards locating their indivisible units in the chromosomes.

These and other conditions have combined to produce two opposing views and the chromosomes have come to be the chief bone of contention. I shall attempt, therefore, to limit my discussion to this topic, at the risk of appearing to take rather a narrow point of view.

We can trace to the important work of Boveri a great deal in our modern conception of the idea of the chromosomes in heredity and development. We owe to Boveri the current conception of the individuality of the chromosomes; we owe to him the discovery of facts that go to show in a sense the independence of the chromosomes of the cytoplasm in which they lie; and most important of all we owe to him the idea that the chromosomes may be individually different and that development depends on the presence in the cells of samples of each kind of chromosome. Let us take up these points in turn.

Individuality is a word with vague meanings. Boveri has, however, defined very precisely the limited way in which he applies this term to the chromosomes. Whether we agree that the facts show the chromosomes to possess this kind of individuality is a question to be further examined, but admitting differences of view possible Boveri's careful analysis of the situations must excite our admiration and respect. Wilson's expression, the genetic continuity of the chromosomes, seems, however, to better express Boveri's attitude than the word individuality used by Boveri himself so far as the facts of direct observation are concerned; but if we extend this term to include Boveri's deductions from certain experimental work, then the word individuality means something more than genetic continuity.

Applied to the chromosomes, individuality means that the chromosome that passes into the resting nucleus is substantially the same that comes out at the next division. This interpretation has met with some opposition. Every cytologist is familiar with the fusion of the chromatin threads in the resting nucleus. If they fuse, what guarantee is there that they will separate again along the exact lines of union? If the separation is not exact the materials of the chromosomes would, before long, become completely intermixed. It is this difficulty that has created a presumption against the theory of the individuality of the chromosomes.

Despite the supposed objection the fact remains indisputable that in cells where the chromosomes can be distinguished by their distinctive sizes, the same sized bodies emerge after every supposed fusion in the resting nuclei. The most convincing evidence for individuality in this sense is that brought forward by Boveri's study of the position and shape of the chromosomes as they emerge from the nucleus at the two-cell stage of Ascaris. He shows that there is often a remarkable agreement between the chromosomes in the two sister cells which can only be explained on the grounds that the chromosomes have retained in the resting stage the same form and position that they had when they went into the resting nucleus, and this arrangement can be traced back to the way in which the chromosomes divided in the segmentation spindle.

This evidence points to the conclusion that the central part at least of the chromosomes has not been lost by fusion in the resting stage. It is important to note that we can not explain their reappearance after each resting stage by means of the assumption that they differ chemically and segregate according to their kinds of materials, because in each nucleus there are two chromosomes of the same sort, one paternal the other maternal in origin, but identical otherwise. The pairs may lie in any position with regard to each other in the resting nucleus. Hence like chromosomes they might often interlace, and there is no guarantee that later these materials would move into the two original chromosomes rather than concentrate around one of the two centers. It has been suggested by Hertwig and held also by others, especially by Fick, that the formation of the chromosomes and of the network represents a kind of crystallization process that is regulated by the amount of chromatin present. This suggestion also meets with serious objections, for, were it true, we should expect, I think, to find that the chromosomes would assume definite positions with regard to each other. The evidence shows clearly that this is not the case, as seen best when chromosomes of different sizes exist. The arrangement is varied in different cells of the same individual and in only a few cases do certain chromosomes lie in a definite position in the equatorial plate—in the center of the plate, for example, as seen in the spermatocyte divisions of certain insects. We can only fall back, therefore, on the evidence, brought forward by Rabl and demonstrated in the clearest way by Boveri, showing that the position of the chromosomes in the new division is determined by the position of the chromatin in the last division, and assume that in some way the center of the old chromosomes becomes the center of the new.

Putting the facts together, they go far towards showing that the central axis of the chromosome is not lost in the resting nucleus, but remains to become the center of the next chromosome. Here perhaps we find a clue to the genetic continuity, or individuality. If we look upon the spinning process of the chromosome as a process by means of which its peripheral substance is thrown out into the nucleus to form the reticulum, and assume that most of it fails to return the next time the chromosome becomes distinct, we have an hypothesis in conformity with many facts at least, and also a view that makes simpler, perhaps, our interpretation of the meaning of the process. On this view the materials set free by the chromosomes remain behind in part when the nuclear wall is dissolved, and become a part of the cytoplasm of the cell. In this way chromatin materials set free at each breaking down of the nucleus reach the cytoplasm, and in time may come to represent a large part of the cytoplasmic substance. If we look upon the chromosomes as organs for producing the fundamental organic material out of substances absorbed by the cytoplasm—in a word if we look upon the chromosomes as assimilating centers of the cell we can understand the enormous increase of chromatin in the early stages of development of the embryo, and also how in time their products set free in the cell may come to have a controlling influence on the reactions and responses of the cytoplasm of the cells.

Any one who has observed the dissolution of the enormous germinal vesicle will sympathize with such an interpretation. A relatively large part of the nucleus is thrown out into the cell; for, the chromosomes form a relatively small part of the entire germinal vesicle.

The impression, often given in popular works on the cell, that the nuclear sap alone is set free at the dissolution of the nuclear wall, and that this nuclear sap is only a watery fluid without significance in the cell, is probably erroneous. On the contrary, there is set free not only a fluid, but a large mass of material that may in part represent some of the nuclear network, and much of this material at once assumes the same staining capacity as the rest of the cytoplasm.

Individuality of the chromosomes means, therefore, in this sense genetic continuity from cell to cell of a portion of each of the original chromosomes. This interpretation will apply whether we consider the chromosomes as made up of entirely different materials, or of partly different materials, or even if they are all identical in chemical composition. Let us turn then to the next most important question. Have we evidence to show whether the chromosomes are identical in chemical composition or whether they are different?

We may dismiss at once, I believe, the evidence based on the similarity of the staining capacities of the chromosomes. With the rarest exceptions they all stain alike. Such methods as are used are too crude to throw any light on the question of their possible differences.

The stains that we employ do little more than differentiate basic from acid bodies and in this regard the chromosomes belong to the acid group. Their finer differences, if such exist, would not appear by the methods used.

The most striking evidence that can be cited to show that the chromosomes are different is based on their size relations. These are constant. Does this mean that the chromosomes are therefore different? I do not believe that such evidence is of any value one way or the other. If the size of the chromosomes is referable to their genetic continuity, the facts can be accounted for without recourse to the assumption of chemical difference.

Fortunately we have some evidence from embryology that has seemed to many embryologists to indicate that the chromosomes differ in their physiological behavior; from which we may infer that they differ chemically. I refer to Boveri's brilliant experiments with the dispermic eggs of the sea urchin.

When two spermatozoa enter simultaneously the egg of the sea urchin each brings in its own center or aster from which two centers are formed. These two centers form a triaster (one being excluded) or a tetraster about the three pronuclei (two male, one female). When the nuclei dissolve each sets free its 18 chromosomes, producing $18 \times 3 = 54$ chromosomes which are distributed to the three poles of the triaster, or to the four poles of the tetraster. The distribution is, as a rule, irregular in the sense that some centers get more than others. The protoplasm then divides into three or into four equal parts, the axis of division corresponding with that of the egg axis as in normal division.

From these eggs embryos develop; many of them are abnormal, but a few are normal. Normal embryos develop more often from the eggs that divided at once into three, than from those that divided into four. Boveri points out that the chance is greater in the three-fold type that each cell gets at least one set of the chromosomes than in the four-fold type—hence he argues the greater frequency of normal development.

Boveri's chief results, however, were obtained by isolating the three blastomeres of the three-fold type and the four blastomeres of the four-fold type. Under these circumstances one or two or three of the isolated blastomeres may produce a normal embryo, but, as a rule, not more than one normal embryo develops, although as stated, cases of two or three embryos are also found. This result can be explained on the ground that only those blastomeres develop normally in which one full complement or set of chromosomes is present. Boveri concludes that normal development is dependent on the presence of at least one set of chromosomes. Hence the evidence points to the conclusion, he believes, that the chromosomes are different; and that one of each kind must be present to insure a normal process of development.

That the results are not due to cytoplasmic differences is shown by the fact that the plane of first division passes through the axis of the egg, so that each blastomere gets a part of the different regions of the egg. That the result is not due to the size of the blastomere is shown by a comparison with isolated blastomeres of eggs that have divided normally. Moreover, experiments with fertilized egg-fragments show that normal development is not dependent on a prescribed size relation between the nucleus and the cytoplasm.

Other objections that have been raised have also been successfully met by Boveri and I can not but think, therefore, that until more valid objections can be found, Boveri has made good his point.

The experiment of fertilizing non-nucleated fragments of the egg has demonstrated that a single set of chromosomes suffices to produce normal development. Artificial parthenogenesis in the sea urchin has also shown that the single set of chromosomes in the female pronucleus is capable of giving rise to normal embryos. It follows that as a result of normal fertilization a double set of chromosomes is present in the embryo—two of each kind of chromosomes—and this fact is of significance in heredity.

Boveri has added further evidence in favor of his conclusion from an experiment in which normally fertilized eggs are put under pressure just as the cleavage is about to appear. The cytoplasm division often fails to take place. A single cell may sometimes contain two nuclei and such cells not infrequently later form polyasters. These may cause inequalities in the distribution of the chromosomes, and the abnormal development that sometimes follows can be explained in the same way as in the case of the dispermic eggs. Boveri asks what can these cases have in common unless it is the inequality in distribution of the chromosomes.

Driesch has argued that, since in the normal development the plane of bilaterality corresponds with the first (Boveri) or second (Driesch) plane of cleavage, the three-fold or four-fold types may fail to produce this effect at the right moment. But it is not evident, even if it is true that a bilaterality exists in the egg, that the embryo might not still produce it independently of the cleavage. In the case of the four-fold type an opportunity is, in fact, furnished for the normal relation to appear, yet this type produces fewer normal embryos than does the three-fold type. Moreover, the development of symmetrical embryos for the one-half and one-fourth blastomeres shows that the egg has remarkable regulatory powers in this regard. Again radially symmetrical embryos have been produced by Herbst in lithium solutions, yet these do not appear in embryos from dispermic eggs.

This evidence goes far towards establishing in some form the probability of Boveri's argument. It seems to me more cogent and convincing than that brought forward by his opponents. It does not, I think, prove that the chromosomes are entirely unlike and does not, obviously, prove that each character of the embryo is located in a particular chromosome. But the evidence makes probable the view that the different chromosomes may have somewhat different functions, and that normal development depends on the normal interactions of the materials produced by the entire constellation of chromosomes.

Boveri himself is far from ascribing to the chromosomes the intricacies of the Weismannian conception. He has clearly stated that his conception of their individuality does not require that each chromosome represents a distinct character of the individual, or even an exclusive bundle of such characters. He concedes, that whatever it is in them that stands for the characters of the adult may be distributed to all of the chromosomes in some species, and that in different species the materials may be differently assorted.

It should indeed be pointed out that Boveri's evidence seems to prove too much for that form of the particulate theory that ascribes unit characters to chromosomes, for it indicates, I think, that individual chromosomes do not in any sense contain either preformed germs or determinants, or unit characters, or even stand for the production of particular organs in any sense.

Were this the case we should expect the isolated blastomeres of the dispermic eggs to produce different kinds of organs, heterogeneously united. It can not fairly be argued in reply to this point that such development would be a physical impossibility; for, we are familiar with the fact that teeth, hair, bones, etc., may form in various teratomata, and this shows that individual organs may develop independently of the rest of the organism with which they are normally connected. This side of the question has not, I believe, been sufficiently considered by Boveri.

It is true that Boveri has pointed out that embryos that develop from dispermic eggs are often imperfect or asymmetrical and interprets this as due to the inequalities of distribution of the chromosomes. His figures, however, give the impression that the abnormalities are due to imperfections in the relations of the parts rather than to dislocation of organs as his view in the strictest sense seems to require. It should not be forgotten that eggs normally fertilized if kept under unfavorable conditions so that they develop abnormally show similar imperfections. Were his results really due to dislocations, *i. e.,* mal-assortments of chromosomes, we should anticipate a far greater mosaic type of development, I think, than actually appears.

In conclusion we must consider the behavior of the chromosomes at that period in their existence that has seemed to most cytologists the most critical time in their history, especially in relation to their behavior in heredity. I refer to the so-called synapsis, when the total number of chromosomes becomes reduced to one half the number characteristic of the body-cells. The most significant fact in this reduction is that like-chromosomes pair, or unite, as first made probable by Montgomery, and since confirmed on an extensive scale by several other writers, notably by McClung, Wilson, Stevens, Schreiner, etc.

It may appear that we can most easily interpret this process as due to like materials running together or fusing in consequence of the likeness of the materials themselves. But that the process is something more than this seems probable from the fact that such union takes place at no other time in the innumerable resting stages, except at this particular one, just prior to polar-body formation in the egg, and at the corresponding period in the spermatogenesis. The actual apposition of the thread-like chromosomes that has been described by many observers does not suggest a simple physical fusion or running into a lump of like materials, but rather the approach and fusion of definite cell constituents. The line of separation persists for some time in some species, according to certain observers, and may, according to Brauer and others, remain evident until the next division occurs, when the threads again separate to pass to different parts of the spindle.

The mechanism appears to be such, on this interpretation, that like chromosomes are at this time separated and pass into daughter cells. If this is the correct interpretation the process is one of profound significance for students of heredity.

It is true that in most cases a separation between the united pairs can no longer be detected and this has been interpreted to mean that an actual fusion takes place as complete as when two drops of water unite into one. If so there would be no grounds left for assuming when the next division occurs, that the united halves actually separate again; for the splitting might occur along any axis of the double chromosome as far as we know. I should not care to make any dogmatic statements in regard to this question in the present unsettled state of our knowledge; but whether we assume the separation to be along the line of union or whether in any other plane the conclusion will have, as I said, a deep interest for the student of heredity.

There is one additional piece of evidence that may be cited in favor of the non-fusion interpretation. In some insects one pair of chromosomes does not enter into synapsis. These remain apart in the nucleus in some species or simply touch each other without fusion in others. In both cases the pair enters the spindle and its members pass to opposite poles.

Even more remarkable are such forms as Acholla, in which one large chromosome has as its mate five smaller ones. None of them fuse in synapsis, but they meet on the spindle and four go to one pole and one—the larger one—to the opposite.

It may be argued that these cases show that the "purpose" of the synapsis is only to bring together similar chromosomes in order that they may be again separated. It can not be denied that these cases give a certain plausibility to this interpretation, yet they are exceptional cases, and it is unsafe to generalize from them to other chromosomes that we know to behave differently. Moreover, this method of "touch and go" appears to be so much simpler than the elaborate changes involved in synezesis, that one may well ask whether synezesis may not have a deeper significance than the mere apposition of like chromosomes. In fact the process seems well suited to bring into close and intimate fusion the pairs of chromosomes instead of simple apposition as appears in the sporadic instances cited above. The situation calls, at least, for a suspension of judgment until we have more evidence.

The number of chromosomes in closely related forms presents one of the most puzzling problems when we attempt to apply the chromosome view to the facts of heredity. The case of the thread worm of the horse, *Ascaris megalocephala,* is the best-known case. In some localities the worms have four chromosomes for their full number, in other localities only two. The animals are identical externally, and occasionally where both forms exist crosses occur. In such hybrids three chromosomes are found in the embryo, but unfortunately no adult worms have as yet been seen with three chromosomes. Such a worm would offer an exceptional opportunity to study the reduction problem. In other groups similar variations in numbers are known between closely related species. For example, one of the phylloxerans has 44 and another 12 chromosomes, yet the two species differ only in minor points, and every structure in one has its counterpart in the other. If the chromosomes are the bearers of the hereditary characters how can such facts be interpreted?

If we think of each chromosome in the one species as containing the unit characters of a leg, or a wing, or an eye, how are the same characters distributed in the other species? Evidently a complete redistribution of such units must be conceived. If genetic continuity is to be extended also to the origin in time of the unit characters in species, it seems to me inconceivable that so vital a question as the assortment of these characters should so readily change in closely similar, and probably closely related species. Difficult as it is to interpret this relation, the simplest view would be to assume that it makes no difference how the chromatin is assorted in the chromosomes, so long as the sum total of the materials is present.

From this point of view the individuality of the chromosomes is a matter of secondary importance; for, the same or equivalent material may be represented by two or by forty chromosomes. Individuality or genetic continuity (*i. e., ontogenetic* not phylogenetic) has no further significance, from this standpoint, than that it insures for each species the transmission to all the cells of the body of a given amount of materials or possibly a definite amount of all the different kinds.

We may next proceed to examine into the relation of the chromosomes in Mendelian inheritance from the point of view reached in the preceding discussion.

Chromosomes and Mendelism

It has become generally accepted by students of Mendelian inheritance that some kind of "segregation" is the key to the numerical results that play an all-important part in the Mendelian theory of heredity. The discovery that there occurs in the formation of the germ-cells a process that supplies the machinery by means of which segregation might take place has aroused expectation to a high pitch of interest in the application of the observations of cytology to the conclusions in regard to Mendelian segregation. It is true that there is much diversity of opinion as to the value of cytological study, in its present imperfect state of development, to Mendelism, and this divergence relates unfortunately to the very nature of the processes involved.

Mendel realized that the numerical proportions that appear in the second hybrid generation could be explained, if, in the formation of the germ cells or gametes, a separation of the constituent elements, or characters of the hybrid occurs. These paired characters that separate Bateson has called allelomorphs.

A process takes place in the germ-cells, at the so-called maturation divisions, that may possibly offer a clue as to how the paired characters in the germ cells of the hybrid separate. Prior to this division there are two chromosomes of each kind; one member of each pair being maternal in origin and the other paternal. The members of each pair come together just before maturation division, reducing the number of chromosomes to half. Later these paired chromosomes divide so that each germ-cell gets one half of each pair.

Sutton first pointed out in 1903 that if each character that mendelizes is carried by a particular chromosome the mechanism of reduction gives an explanation of the way in which there may come to be two kinds of germ cells with respect to each particular pair of characters. This hypothesis has been championed by Wilson in 1903, and later by Boveri in 1904.[1] If we analyze the facts further we find that the hypothesis requires in order that pure gametes are to be formed by the hybrid that each particular character, or whatever it is that produces the character, be confined to a single chromosome; otherwise the separation will not be complete and pure gametes will not be formed. Do the facts of reduction fulfil this condition?

When the reduction in the number of the chromosomes takes place we find that the homologous pairs of chromosomes fuse completely, so far as we can judge by our modern methods of technique. Observation gives no evidence in most cases that the chromosomes only adhere side by side, but on the contrary conjugation appears to be a complete fusion, and if this is what really takes place, what guarantee is there that subsequently the members of a pair will separate along their line of fusion? It seems all the more remarkable that such a process should take place, if, as is often assumed, the separation division is not the first, but the second division of the paired chromosome. In other words it is admitted that in such cases the first division is at right angles to the plane of union, and that only at the second division does separation or segregation occur. In fact the assumption of separation is largely gratuitous, and is the outcome of certain theoretical postulates of Weismann's theories—postulates that rest in part on questionable evidence.

---

[1] In 1902 Boveri referred to a possible relation between reduction and inheritance in hybrids, but he did not point out how this idea could be applied to explain the numerical results of Mendelism.

All that we really know is that in some cases two longitudinal divisions of the chromosomes occur,[2] whose relation to the plane of fusion is largely hypothetical. If, however, it be assumed that the chromosomes simply come to lie side by side (or even end to end) and later separate the process of synapsis, as it is called, is merely "touch and go" and has no deeper significance. If, on the other hand, it be assumed that the synapsis is a true fusion of the combining elements, there are no reasons to suppose that the chromosomes separate later into their constituent parts. The expectation is rather that once completely fused they do not necessarily separate at the plane of fusion to give the pure elements that combined.

It is, however, the assumption that the chromosomes do separate along their line of union that has appeared to some writers to have important bearing on the theory of Mendelian theory of pure gametes. Let us therefore assume for the moment that the separation takes place in this way. Since the number of chromosomes is relatively small and the characters of the individual are very numerous, it follows on the theory that many characters must be contained in the same chromosome. Consequently many characters must Mendelize together. Do the facts conform to this requisite of the hypotheses? It seems to me that they do not. A few characters, it is true, seem to go together, but their number is small, and it is by no means evident that their combination is due to a common chromosome. It is true that in no one species do we know much concerning the behavior of many characters, but so far as we do know them there is no evidence that they Mendelize in groups commensurate with the number of chromosomes. In two cases, in fact, viz., in *Pisum* and in *Antirrhinum* it appears that the number of the characters that have been shown to Mendelize separately is greater than the number of their chromosomes.

---

[2] For the sake of simplicity I have left out of account here the possibility of end-to-end union.

This has seemed a fatal objection to the chromosome view, but it may not be so, as Spillman has argued, so long as it has not yet been shown that all of the dominant characters may be present at the same time. But even admitting this possible way of eluding the objection, the other point raised above concerning the absence of groupings of characters in Mendelian inheritance seems a fatal objection to the chromosome theory, so long as that theory attempts to locate each character in a special chromosome. We shall have occasion to return to this point later.

In recent years most workers in Mendelian inheritance have adopted a new method of formulating their theory. Characters that Mendelize are no longer allelomorphic to each other, but each character has for its pair the absence of that character. This is the presence and absence theory. We can apply this hypothesis to the chromosome theory. For examples, let us assume a new variety or race arises by the loss of a character from that chromosome that has heretofore carried it. The chromosome still remains in existence, since it may carry many other characters besides the one that was lost, and it becomes in the hybrid the mate of the one still retaining that character. If now separation occurs, two classes of germ-cells result, one with and the other without the character; and the observed numerical proportions follow. There is nothing in this assumption that meets with any greater difficulty on the chromosome separation hypothesis than on the earlier view of paired allelomorphs, but it meets with the same difficulties, and as an assumption is neither more nor less in accord with the postulated mechanism.

More recently, still another interpretation has been suggested by Shull and by Spillman. It is a quantitative conception, and I shall try to point out some of its applications to the chromosomes.

Let me recall once again the familiar fact that in animals and plants two homologous chromosomes of each kind are present in every cell. This gives the diploid number. One of each kind suffices to produce the character in some cases, but each is nevertheless present in double. We might think of the doubleness as a sort of reserve and the double group be conceived as a "mechanism of safety." That the double number is not always necessary for the formation of the characters is shown in embryos that develop from non-nucleated fragments of eggs. These embryos have all the characters peculiar to their species. The importance of the double set is illustrated, however, in certain hybrids. The best case is that of the hybrid between horned and hornless races of sheep. The male hybrids from this union have horns, the female hybrids lack horns, irrespective of the way in which the first cross was made, *i. e.*, the results are the same whether the mother was horned and the father hornless, or the mother hornless and the male horned. Bateson interprets this to mean that one dose of horns in the male hybrids suffices to call forth horns; but one dose in the female hybrids is insufficient to call forth horns. In terms of chromosomes this may mean that one horn-bearing chromosome suffices in the male to call forth horns, but in the females one chromosome is not enough.

When these hybrids are inbred they produce in the second generation four kinds of individuals, horned males and females; hornless males and females. The numerical results appear to coincide with the assumption made above in regard to the number of doses of chromosomes necessary to call forth horns in the two sexes. For in the second generation there will occur a certain number of combinations in which females will contain two doses of horns and these females should be horned.

The case of color blindness in man appears to follow the same rule, for here also females may transmit the character without developing it, while males, if they have it at all, develop color blindness. One dose of color blindness in males makes the male color blind; one dose in females is insufficient. The rarity of color-blind females is explicable on this view.

These results may be significant for the chromosome hypothesis since the interpretation seems to imply that the amount of a given material, or chromatin, perhaps, is an important element in the determination of the development of characters. If the interpretation is correct it means that a character will not develop even when its primordia or forerunners are present, unless a sufficient amount of that material be present. And, on the other hand, in other individuals a smaller amount of the same material suffices to call forth the unfolding of a given structure.

The same interpretation seems to have a wide application to the characters of the first generation of hybrids, and in all heterozygous individuals that are in nature identical (*i. e.*, heterozygous) with the first generation hybrids. It is known that in several cases the dominant character does not reach its full development in the first generation, as Correns showed for *Mirabilis Jalapa*. Such cases can be explained on the ground that one dose is not enough. The reappearance in the second generation of individuals with the full dominant character is in harmony with this assumption, for in one fourth of the individuals two doses of dominance are expected.

In mice, too, the heterozygous form between black and chocolate often shows black or chocolate areas in the fur, and in the same mouse a region may be at first black and later chocolate, or *vice versa*. It appears that the condition of the mouse at the time when the molt takes place determines whether the hair contains the one or the other pigment in excess. Thus external conditions or internal states may regulate dominance in hybrid forms.

Such facts lead to a consideration of how far quantitative relations are factors in heredity, and how far the chromosomes support such an interpretation. If, as we have seen, the development of a character depends on the amount of a given material rather than on its presence or total absence as the theory of pure gametes demands, may not this view give an interpretation of the rôle of the chromosomes in inheritance?

Let us see where such an interpretation leads. By means of diagram A, I have tried to indicate one way in which a quantitative interpretation of the facts of Mendelian inheritance might be explained. In the hybrid the pair of fused chromosomes, representing the presence and absence of a character, is represented by the black and white semicircles fused together. Should their separation occur along the line of fusion (first line) as demanded by the theory of pure gametes, there will result after two divisions two chromosomes bearing the positive character (or briefly the black chromosomes), and two without (or the white chromosomes). These are represented for the egg in the upper line by the four semi-circles; and the similar cells for the male by the four similar semi-circles in the line below. Chance combinations will give three classes of individuals in the proportion of 1:2:1; or three with the dominant to one with the recessive character.[3]

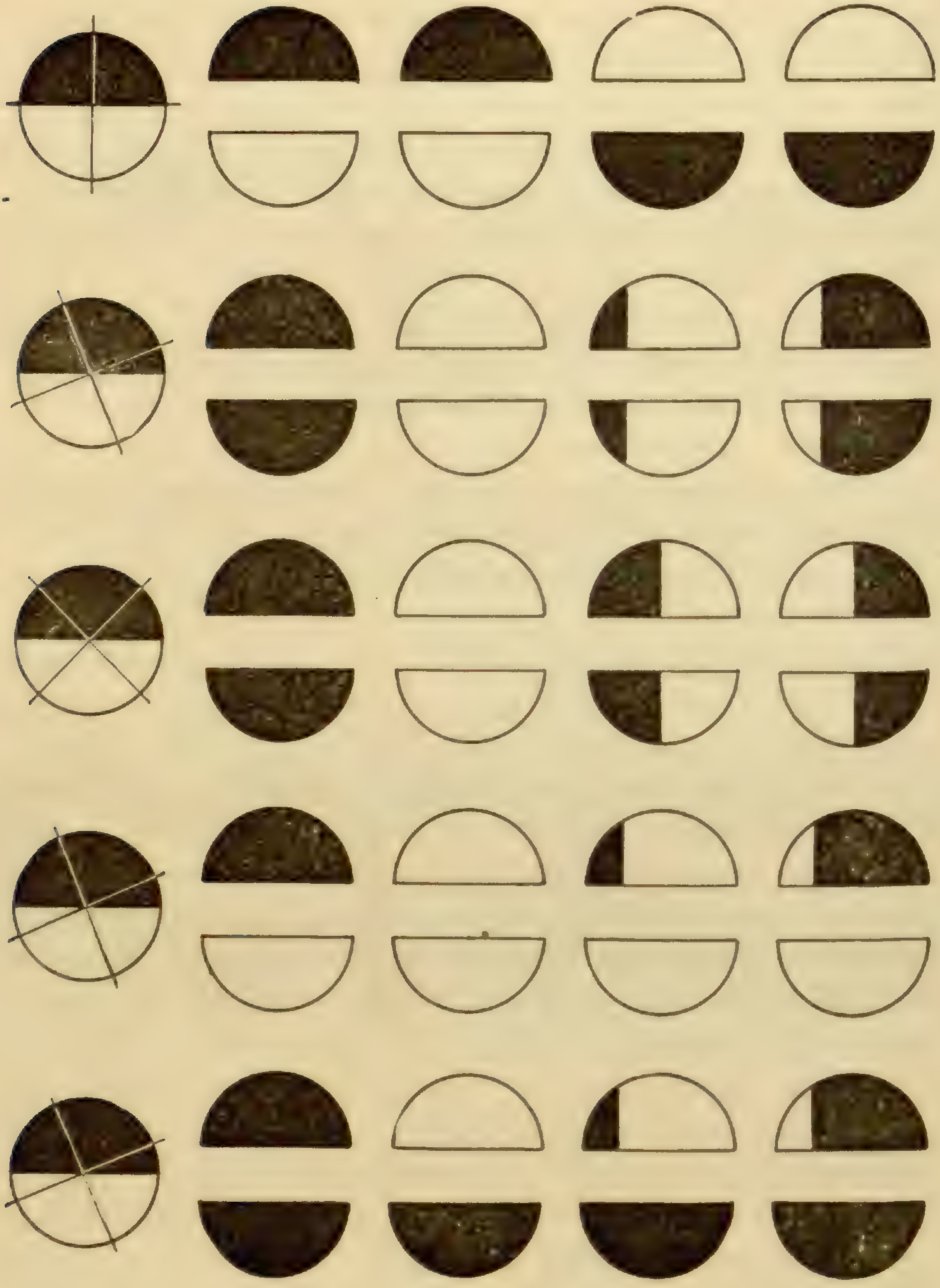
But should the pair of chromosomes fuse and not separate at the line of fusion, the results are shown in the second line, where the intersecting lines indicate the plane of division. Again four classes of gametes result, as shown in the upper line. If the same sort of division occurs in the male, and fortuitous combinations result, there will be the same three classes of individuals as before, which gives the ratio of three dominant to one recessive.[4]

The only division that will not give this result is that

---

[3] In this scheme when one of the two chromosomes of the pair is black the combined action is black.

[4] It is assumed here that when as much or more than the volume of one member of the pair is black the result is black.



when the planes of division lie exactly at 45 degrees to the plane of fusion, as shown in the third line. Here the results give 11 dominant to 5 recessive, but this is so near the three to one proportion that it offers no serious drawback to the result when we consider how seldom this division will occur.

The two remaining lines show the results of back-crossing between the hybrid (F_1) with the recessive (fourth line); and with dominant (fifth line). They give the expected proportions.[5]

In all of the preceding cases except the first the gametes are not pure, as a rule, but nevertheless produce two classes of individuals that may be sharply defined. This scheme seems to work as well as the pure gamete assumption; it avoids certain difficulties encountered by the latter; and appears to explain further a class of cases inexplicable on the pure gamete hypothesis; namely the graded series of forms so often met with in experience and so often ignored or roughly classified by Mendelian workers.

Again, for simplicity it has been assumed that varieties or races lacking a character lack entirely the kind of activity that calls forth that character. But there is no need to make this limitation. If in some cases the lack of character may in reality be due to total absence of action, there are other cases which can be explained on the chromosome basis if we assume that the absence of a character is due to incomplete or insufficient activity of its chromosomes varying from 1 to 50, to put the matter graphically. Let us assume 25 per cent. of activity takes place. Such an individual paired to a dominant will give dominance in the first generation (due to the 50 per cent. of the dominant plus 25 per cent. of the recessive). Chance splitting of the fused chromosomes after synapsis in the hybrid will give two classes of gametes, but one class will contain numerically more than 50 per cent. of character-forming materials. Consequently there will be more individuals of the dominant race than the theory of pure gametes and equal division demands.

The converse case is also worthy of consideration. If one individual is just able to produce a given color or material by the combined activity of its two chromosomes, but no more than just able to do so, and the other individual totally lacks all power, the first hybrids will also fail to produce the character. Their chromosomes combined and divided at random in the germ cell will produce a much larger number of gametes that fall below the standard than of those that rise to a point sufficient to give the character when combined—in consequence the recessives will be greatly in excess.

---

[5] Provided when more than half of a chromosome of a pair is black the result is black.

These considerations may seem to throw light on the question of potencies of different individuals—a question that is coming more into the foreground. We can see from the point of view here suggested how individuals alike externally may differ very greatly in their power to transmit their peculiarities to hybrid offspring.

This conclusion is especially applicable to cases where the full development of a character can only appear when two groups of chromosomes (to take the simplest case) are necessary to produce a character; or, to take the more extended view, when excessive amounts of chromatin must be present. It is now well established that certain races lacking a character nevertheless dominate in the first generation when crossed with a race possessing a character. In such cases the failure of dominance may be due to insufficient chromatin of the positive kind rather than due to an inhibiting factor as sometimes assumed.

As regards blending, it is evident that this relation must result from the combined action of the two parental contributions to the hybrid; the blending is the sum of both effects. Such cases differ from Mendelian cases in the first generation only in that one influence does not exclude the other. In the second generation separation into two classes of individuals does not occur, but a great variety of forms appear: Nevertheless the individuals may show a tendency to group around the two parental and the hybrid classes, as Castle has shown for long and short hair. In this sense blended inheritance shows gradations into alternate inheritance. The chief difference between the two, I repeat, is found in the compatibility of the contrasted characters. So far as the chromosomes are concerned the results need not be referred to any special kind of fusion of the combining elements, but simply to the way in which the effects become patent. Alternate inheritance and blended inheritance appear only to be extremes of the same process.

This brings us to the inheritance of the spotted condition, a class which has been a serious difficulty on the assumption of Mendelian dominance and segregation of pure characters. The most striking case is that of spotted animals or striped plants. Some regions of the body are colored, other regions white, *i. e.,* they lack pigment. On the assumption that the individual has the capacity to produce pigment the presence of white spots is inexplicable; on the assumption that the individual lacks the power to produce pigment the colored spots are inexplicable. A spotting factor is therefore assumed whose presence accounts for spots. Its allelomorph is a uniform coat whose presence does away with spots. A more refined juggling would be difficult to imagine, especially when the presence of color is explained by the presence of an enzyme and a color producer, and its absence to the lack of one of these. Yet after appealing to a purely physiological principle to explain color versus no color, the explanation is thrown overboard in the case of spotted animals and a mystical spotting factor is set up as an explanation. The humor of the situation grows when one thinks that the spotting factor may produce a few white hairs on the tip of the tail, or a coat nearly entirely white. To be logical there should be as many spotting factors as there are hairs on the body.

It has been shown that the spotted condition does not follow by simply crossing a uniform color and an albino —unless that albino has been derived from spotted ancestors. Hence spotting is not due to combinations of this sort, but is due to a condition peculiar to certain races. How can we interpret this peculiarity? The great difficulty of explaining this class of cases must be admitted, but I think that a possible interpretation may be found in the following direction, although I am far from wanting to urge that it is the only possible interpretation. The absence of a character, color in the present instance must be due to local conditions; certain regions are like the hornless female hybrid sheep. It is well known that injuries to the skin may cause the cessation of formation of colored hair and the production of white hair. Similarly in colored animals, certain regions are more prone to lack pigment than other regions. In rodents for example, the belly, the tip of the tail and the forehead seem to be such regions even in animals that would be classed as uniformly colored. It follows that if in certain races these regions are particularly deficient in their power to produce pigment a spotted race will arise. Crossing with an albino race does not increase the extent of the spotted area in the hybrid. On the contrary, if the white animal has been derived from a race uniform in pigment production in these regions the hybrid will be uniform, *i. e.,* not spotted at all, although one parent was spotted.

It may appear that this view has simply introduced the spotting factor in a new guise. In a sense this is true, but it recognizes a condition that is ignored by those who make use of a spotted factor, for it rests on the assumption that whether pigment develops in certain regions depends not only on whether pigment producing factors are present or absent in the germ cells, but on the modifications of such inheritance by local conditions. My conclusion is, moreover, of a piece with our general knowledge of development of different organs of the same embryos.

Why, it may be asked, can not the spotted character be explained on the assumption of weakened power in these spotted races to produce color; or why is it not due to loss of chromosomes in the early blastomeres of the germ cells in certain regions?

The first alternative must be rejected, I believe, for were the power of color production weakening in spotted animals, the ratio being lower than 50 per cent., we should still have to invoke local action to account for the results.

Moreover, there is no evidence that color production is less intense here.

The other alternative can be answered on more general grounds. If Mendelian characters are due to the presence or absence of a specific chromosome, as Sutton's hypothesis assumes, how can we account for the fact that the tissues and organs of an animal differ from each other when they all contain the same chromosome complex. Bateson has called attention to this weakness of the single-chromosome-single-character hypothesis. For on such a view the chromosomes should be sorted out in the soma until each region gets its proper kind. The facts are the reverse. However important therefore the chromosomes are in transmitting the full quota of hereditary traits, we must be prepared to admit that the evidence is entirely in favor of the view that the differentiation of the body is due to other factors that modify the cells in one way or in another. This consideration is, to my mind, a convincing proof that we have to deal with two sets of factors—the common inheritance of all the cells to produce all the kinds of tissues and organs in the body, and the limitation of that property in the course of development. If the former is due to the chromosomes and the unspecialized parts of the cytoplasm, the latter may be due to the local changes that the relation of the parts to each other calls forth. It might even be argued that since in the development we find no evidence of a sorting out of the chromosomes that produce special parts, the individual chromosomes can not stand each as the representative of those parts, but rather that each part needs the entire set of chromosomes for its normal life. However tempting such an argument may be for those who have reached on other grounds the conclusion that this is the more probable interpretation of the chromosomes, the argument will not appear conclusive to those who do not accept such a general standpoint, for they may justly claim that we know too little about the possibilities of chromosomal behavior to make this sort of a demand of them. The consideration is nevertheless, I think, worth consideration.

The most serious, and probably fatal, objection to the quantitative view outlined above is found in the later possibilities of the mixed chromosomes. If the longitudinal division is fortuitous in the synaptic pair it must also be assumed to be fortuitous in the later splittings of the same chromosomes in the embryo. The results would give a mosaic of cells in some of which one and in other cells another character will predominate. We should expect therefore a sort of piebald or chimaera type to result. The difficulty is not minimized by referring the results to all of the chromosomes instead of to a single one.

Unless we refer the problems of heredity to principles apart from a material basis our only hope at present of a scientific solution of the problem is to rely on such a basis. There are three ways, however, in which we may make use of such a physical material conception of "segregation." First, by postulating material particles in the chromosomes of the germ cells qualitatively different—particles that are sorted out at the reduction period. Our analysis has shown that there are serious difficulties for this interpretation. Second, by postulating a quantitative factor as the basis of segregation; here also difficulties are met with. Third, by assuming initial differences in the germ cells of the hybrids due to the same kind of differences that become patent in the development of the embryonic organs where the results are not referable to segregation of chromatic materials, but due to regional differences or state of equilibrium—the result of reactions between the cells. Here it seems to me we find the most promising direction in which to look for further light on the subject. For example, the formation successively of brown, yellow and black pigment by the follicle cells of a gray mouse suggests that a similar process may take place in the germ cells of hybrids. In the somatic cells no one supposes that the differences are due to loss of chromatin, or to a segregation, otherwise, of materials. On the contrary, the presumption is in favor of the view that the effects are produced not by segregation, but by the relation of the cells to each other, or to the whole. If this comparison be admitted, it follows that at some stage in the history of the germ cells of the hybrid similar effects may take place in regard to each kind of the inherited qualities (not characters). In this connection it should be recalled that the germ cells of the hybrid have had a long history before maturing. If the chromosomes are the essential elements in producing or maintaining the material constitution of the cells there has been an abundant opportunity for the chromosomes to have produced general effects of this kind. The way in which the cells react will depend on the changes that the chromosomes have produced in them. In other words, at some period in their history when the germ cells have become, as it were, hybrid throughout they develop one or another of each of the alternate possibilities to a greater or to a less degree. Since the same sort of process occurs in groups of somatic cells where it results from the responsive action of the parts on each other, so let us suppose in the germ cells of the hybrid a similar relation determines the fate of its different potentialities.

Our general conclusion is, therefore, that the essential process in the formation of the two kinds of gametes of hybrids in respect to each pair of contrasted characters, is a reaction or response in the cells, and is not due to a material segregation of the two kinds of materials contributed by the germ cells of the two parents. The reaction differs in the germ cells of the hybrid from that of either of the parental types because the material basis of the germ cells differs owing to its dual origin. The results are due, however, to difference in reaction, and not to a separation of mixed materials. The general point of view that underlies this conclusion is epigenetic, while the contrasting view, that of separation of materials, is essentially one of præformation.

CHROMOSOMES AND SEX.

In recent years two converging lines of evidence have led the most sanguine of us to hope that before long we shall know, in part, at least, the answer to the outstanding riddle of the ages, the determination of sex. These two lines of research are the experimental study of sex inheritance, and the microscopic study of the germ cells. Both have led to the conclusion that sex is not, as has been so often supposed, determined by the external conditions to which the parents, or the eggs, or embryos are subjected, but that there exists an automatic process in the egg and sperm by which equality of the two sexes is attained.

Before I bring this evidence forward, I must stop for a moment to point out how the idea that sex is determined by external conditions arose, for this view is by no means defunct. In fact it is a widely current belief at the present time. One might, in fact, appear to justify himself in holding such a view, not only by quoting the names of those who have advocated it or still maintain it, but even by referring to a considerable number of experiments that have been claimed to be in favor of such an interpretation.

Landois stated in 1867 that he could produce male or female butterflies at will by regulating the amount of food of the caterpillars. Similar statements were made later by others; but the futility of the experiments became manifest when it was found that the character of the sexual organs is already determined when the caterpillar hatches from the egg.

It has been claimed that the sex of the frog could be determined by the quantity of food, or by the kind of food supplied to the tadpole. More extensive work has disproven completely this statement also.

Statistical studies, especially those of Düsing, are often cited to show that in man, and in some of the domesticated animals, the nourishment of the parents affects the sex of the offspring. But here again other statisticians have found evidence of the opposite results.

The careful experiments of Cuénot and of Schultze on mice have positively shown that no such relation exists in these animals.

There are two groups of animals that seemed for a long time to furnish evidence in favor of the view that sex is determined by the environment. I must refer to these in more detail.

The plant lice, or aphids, produce throughout the summer by means of parthenogenesis a series of parthenogenetic females. In the autumn, when the food begins to fail, there appear males—and *sexual females.* If the aphids and their food plants are brought into the green house the males and sexual females may not appear, but the animals go on reproducing by parthenogenesis. It seems, therefore, that external conditions determine the appearance of males and are therefore sex determining, since the parthenogenetic forms are ranked as females.

It has become apparent in recent years that these results have nothing to do with sex determination in the sense that external conditions determine the production of males or females. The results show that external conditions cause the cessation of the parthenogenetic reproduction and the beginning of sexual reproduction, *i. e.,* the appearance of males and sexual females. Whether the one, or the other, seems not to be determined by the environment, but to some internal mechanism to which I shall refer later.

In the rotifer, *Hydatina senta,* Maupas claimed that temperature determines sex. Later Nussbaum tried to show that food conditions determine sex in this animal. Still more recently both views have been disproven. It has been shown in the first place that here, as in the aphids, the external conditions affect the life-cycle in such a way that parthenogenesis ceases and sexual reproduction begins. Recently A. F. Shull has determined that if the animals are kept in old culture water, *i. e.,* water in which the food has been kept—parthenogenesis goes on indefinitely. At least nineteen generations of purely parthenogenetic individuals have been reared.

But if at any time individuals are taken out of this culture medium and put into spring water, males and sexual females appear. By diluting the spring water with varying amounts of culture water the number of sexual forms that appear is directly proportional to the dilution.

In this animal the individual that produces the male eggs is the same individual that produces the sexual egg. If she is early fertilized by a male, her eggs produce sexual females. It is clear here that external conditions change the cycle but do not determine sex. This brief review will suffice to clear away the traditional evidence supposed to support the view that sex is determined by the environment.

Let us pass now to the results that seem to show that there is an internal automatic mechanism that regulates the production of males and females. I shall take up the botanical evidence first.

Correns' experiments with two species of *Bryonia,* may be examined. *Bryonia dioica* is diœcious; *B. alba* monœcious. Correns' main experiment shows that when *dioica* ♀ is crossed with *alba* ♂, all of the offspring are females, but when *alba* ♀ is crossed with *dioica* ♂, half the offspring are male and half female. The results can be explained by three assumptions. First that the male condition dominates the female, second that the diœcious condition dominates the monoecious; third, that the female is homozygous in regard to sex and the male heterozygous.

These conclusions are opposed to the interpretation of other workers that make the female the dominant condition. It is also not clear from G. H. Shull's recent work on a more extensive scale that the diœcious condition can be assumed in general to be dominant.

Whatever the correct interpretation may be, these facts show at least that by treating sex as a character that segregates in the gametes, as Mendelian characters in general are assumed to do, the results can be accounted for, provided one sex is assumed to be always heterozygous and the other homozygous.

The experiments of Elie and Emile Marchal on diœcious mosses are equally interesting. They used species with separate sexes. When spores from a single capsule are sown some produce female, others male protonemata. The sporophyte generation that produces the spores has arisen from a fertilized egg; the formation of the spores is a non-sexual process. The sporophyte contains the full number of chromosomes, and this number is reduced to half in each spore, not by union of chromosomes, but by halving the total number.[6]

The protonemata or gametophytes produce the male or the female organs separately. Fragments of a protonema regenerate a new individual having always the same sex, under all the possible external conditions to which the Marchals subjected them. Obviously the sex of the protonema *once* determined can not be changed, and the presumption is in favor of the view that the sex of each spore is determined at some time in its formation.

The tissues of the sporophyte itself should contain the potentiality of both sexes. Owing to the power of regeneration possessed by this tissue, it is possible to test such a view. Pieces of the sporophyte regenerate protonemata—each thread arises from a single cell of the piece; a cell presumably having the full number of chromosomes. These regenerated protonemata produce moss plants that are either male, or female, or hermaphroditic. They seem to be all potentially hermaphrodites, but in some plants only the male organs develop—especially those that first appear; in other plants only female organs. If the suggestion just hazarded is correct, namely, that all the plants are hermaphroditic, and the males and females are due to the failure of the other sex to develop, we raise a large issue; namely, whether males and females may not in general be potential hermaphrodites with only one sex developed, or whether the sexes are separated into pure male and pure female forms, as is assumed in so many of the most recent speculations concerning sex. This topic will come up later for fuller consideration.

---

[6] Although union may have preceded the reduction in number as in ordinary synapsis in plants and animals.

As I said, the presumption is that the regenerated protonemata from this sporophyte have the diploid number of chromosomes, and when the spores are formed the number is reduced. Have the sex characters separated when the chromosomes are reduced? We have no means of knowing, but two important points should be noted: first, that the male or the female is produced with the reduced number of chromosomes present; second, that an approach to the same result is reached in the regenerated forms with the entire number present. Sex here is not connected with the half number, or the whole number. Any attempt to solve the problem of sex in the mosses along these lines must assume that some unknown or unseen chromosomal element is separated at the time of formation of the spores.

Furthermore, since hermaphroditic species of mosses and ferns produce both male and female gametes on the same plant that has the reduced number of chromosomes, it would be necessary to assume in such cases that some kind of chromosomal separation takes place in different regions of the same protonema to give rise to male or to female organs. The only other alternative would be to assume that the kind of gamete formed, male or female, is determined by the regional differences in the protonema or prothallium, and that no separation of chromatin precedes this effect. If such effects can be produced in this way, may it not be that similar processes occur in the unisexual species? I shall return to this topic again.

Blakeslee's brilliant experiments with moulds also bring out many important points connected with sex determination, although nothing is known as yet concerning the changes in the chromatin. He finds in Phycomyces that some mycelia are male (or — strains as he calls them) and that these produce non-sexual spores of the same sex indefinitely. Other mycelia are female (+

strains) and produce only female spores. Male mycelia will not conjugate with mycelia of the same sign, but readily with the female mycelia. In fact, their sexual behavior is the only way of distinguishing the two kinds of mycelia. On the other hand, the sexual spore or zygospore produces a sporophyte that in turn produces spores; some of which are male, others female.

In striking contrast to this case is that of *Mucor mucedo.* Here also male (—) or female (+) mycelia are found which unite to form the sexual spore. This produces the sporangiophore bearing a sporangium whose spores are all of one or of the other sex, *i. e.;* all the spores from the single sporangium give rise to males; all the spores from another sporangium gave rise to females. Despite the fact that the zygospore is formed by the union of the two mycelia, male and female, the spores are not mixed, but represent only one sex. Blakeslee points out that this is the same condition found in diœcious flowering plants, such as the Lombardy poplar, when one seed gives rise to a male tree, another seed to a female tree. In these cases the evidence points to the view that there is no separation of sex units, but a suppression of one sex or the other. In other words that the basis of sex is the hermaphrodite condition and the unisexual form is due to the suppression of one of the dual possibilities, and not to a separation of unit characters that stand for male and female.

Let us next turn to the experimental evidence in the animal kingdom. Since the experiments of Doncaster and Raynor on the current moth, *Abraxas grossulariata,* bid fair for years to come to occupy the foremost place in speculations concerning sex I shall bring forward this evidence first.

This species has a rare sport known as *Abraxas lacticolor.* No intermediate forms between the two exist and none arise from crossing. In nature female specimens only of *laticolor* have ever been found, although males have been produced artificially by suitable combinations, as will be seen below.

No less than four hypotheses have been already advanced to explain these facts. Doncaster assumed, at first, that each sex produced male and female gametes; that in the first hybrid generation the male gametes bear the *grossulariata* character and the female the *lacticolor;* that in the male no such coupling occurs. Bateson and Punnet simplified this hypothesis by assuming that the female is heterozygous for sex, the male homozygous; that femaleness is dominant to maleness; that in the hybrids the character for femaleness and that for *grossulariata* repel each other so that each germ cell gets one or the other. The results are summed up in Table I.

TABLE I

Abraxas crosses, Doncaster's Interpretation

	Parents.	Constitution.	Gametes.	Offspring.
Cross 1	Lact. female Gross. male	LL♀♂ GG♂♂	L♀, L♂ G♂, G♂	GL♀♂ = gross. female GL♂♂ = gross. male
Cross 2	Heterozygous female Heterozygous male	GL♀♂ GL♂♂	L♀, G♂ G♂, L♂	GL♀♂ = gross. female LL♀♂ = lact. female GL♂♂ = gross. male GG♂♂ = gross. male
Cross 3	Lact. female Heterozygous male	LL♀♂ GL♂♂	L♀, L♂ G♂, L♂	GL♀♂ = gross. female LL♀♂ = lact. female GL♂♂ = gross. male LL♂♂ = lact. male
Cross 4	Heterozygous female Lact. male	GL♀♂ LL♂♂	L♀, G♂ L♂, L♂	LL♀♂ = lact. female GL♂♂ = gross. male

Castle pointed out that Wilson's sex-hypothesis, that two X chromosomes stand for femaleness and one X for maleness, will not explain the case of *Abraxas,* but that by the hypothesis of one X standing for femaleness and no X for maleness, the results can be explained; provided Bateson's assumption of repulsion is also employed. Thus if in the Bateson-Punnett table (above) the male signs are omitted, and X put in for the female signs, the results just stated follow, as the next table shows. It will be observed that Castle has simply omitted the male and female signs and substituted X for femaleness. When it is absent the male is assumed to develop.

TABLE II

	Parents.	Constitution.	Gametes.	Offspring.
Cross 1	Lact. female Gross. male	LLX GG	LX, L G, G	GLX = gross. female GL = gross. male
Cross 2	Heterozygous female Heterozygous male	GLX GL	LX, G G, L	GLX = gross. female LLX = lact. female GL = gross. male GG = gross. male
Cross 3	Lact. female Heterozygous male	LLX GL	LX, L G, L	GLX = gross. female LLX = lact. female GL = gross. male LL = lact. male
Cross 4	Heterozygous female Lact. male	GLX LL	LX, G L, L	LLX = lact. female GL = gross. male

More recently Spillman has suggested a simpler explanation that avoids in a sense the postulate of repulsion of femaleness and *grossulariata*. According to Spillman, if the character for *grossulariata* be represented by "G" and femaleness by "X," then if G (or L) and X when they meet behave as ordinary allelomorphs, the results can be accounted for. The next table shows how Spillman's scheme applies to *Abraxas*. It is apparent that he has further simplified Castle's table by omitting one L whenever it occurs with another G or L. This arrangement avoids the necessity of the assumption that femaleness is repelled by X (as on the Bateson-Punnett scheme) because the X that was repelled has become the allelomorph of the G that is present and allelomorphs are supposed to move to opposite poles.

TABLE III

Parents.	Constitution.	Gametes.		Offspring.
Lact. female Gross. male	LX GG	L G	X G	GX = gross. female GL = lact. male
Heterozygous female Heterozygous male	GX GL	G G	X L	GX = gross. female LX = lact. female GG = gross. male GL = gross. male
Lact. female Heterozygous male	LX GL	L G	X L	GX = gross. female LX = lact. female GL = gross. male LL = lact. male
Heterozygous female Lact. male	GX LL	G L	X L	LX = lact. female GL = gross. male

It will be observed that in this table the "heterozygous female" is GX. She is therefore not heterozygous for *lacticolor* unless *lacticolor* is absence of G.

The case of *Abraxas* finds a parallel in three characters in fowls and one in canaries.

The pink eyed cinnamon canary crossed with the black eyed green canary gives the following results:

P. ♀ × B. ♂ = 100 per cent. Black eyed ♂ + ♀,
B. ♀ × P. ♂ = 50 per cent. Black eyed ♂ + 50 per cent. Pink eyed ♀ + 4 per cent. black eyed ♀.

Analysis shows (if we reject the 4 per cent. unexplained anomaly), that the facts can be explained in the same way as in *Abraxas*.

The barred condition of the feathers of Plymouth Rock fowls is inherited in the same way as the next table shows when crossed with Langshan.

Ply. ♀ × Lang. ♂ = 50 per cent. Ply. ♂ + 50 per cent. Lang. ♀,
Lang. ♀ × Ply. ♂ = 100 per cent. ♂ and ♀.

There are two varieties of Game Bantams which according to Hagerdoorn give similar results.

Bankiva ♀ × Brown red ♂ = 50 per cent. Bankiva ♂ + 50 per cent. Brown red ♀,
Brown red ♀ × Bank. ♂ = 100 per cent. Bankiva ♂ and ♀.

Finally yellow shanks and blue shanks in fowls are inherited apparently in like fashion.

Yellow ♀ × Black ♂ = 100 per cent. Yellow ♂ and ♀,
Black ♀ × Yellow ♂ = 50 per cent. Yellow ♀ + 50 per cent. Black ♂.

These facts are of extraordinary interest, for they show that certain characters behave in certain ways that can be explained on the Mendelian formulæ provided that sex is likewise treated in the same way.

It may seem unfortunate that we have so many possible ways of explaining the same facts, and the case might be turned to ridicule on that score, but the explanations are only variations of the same hypothesis. Whatever the final decision may be it is interesting and important to find that the inheritance of sex can be treated by the same methods used for other alternate characters and gives consistent results. Let us be as sceptical as we will, yet the facts will impress themselves on any one who takes the pains to think them over.

Such are the experimental results. Looked at not too critically they show that by the time that reduction of the chromosomes occurs, or after that event, there seems to exist a distinction between the cells, so that half of the cells are destined to become males and half females. But, as has been said, unless we assume this process to take place in one sex only the results can not be explained.

Let us turn then to the evidence which the study of the germ cells has revealed, which shows that in certain forms exactly such a process occurs in one sex and not in the other. I may say at once that the evidence relates to the chromosomes of germ-cells.

Only a few years ago it was generally held that the number of chromosomes in each species of animals is constant for all individuals of the species. Every cell in the body contained the same number.

We now know, however, that in some species of animals, the female contains one more chromosome than does the male, and we have a complete account of the mechanism by means of which this difference arises.

In *Anasa tristis* and in *Protenor*, and in a number of other insects, as shown by Wilson, one chromosome in the male has no mate. At one division it passes to one pole of the spindle, so that one of the two resulting cells has one more chromosome than the other. This chromosome is the accessory, or the odd, or the sex chromosome, or, as Wilson has called it, the X-element. At the other division it, like the other chromosomes, divides into two parts, so that both of the derived cells from this division have the same number of chromosomes. In the egg the X-element has a pair, another X to all appearances. Thus there are two X's in the unripe egg, and one in the sperm-mother cell. These three are apparently identical, and their perturbations I have called the problem of the three chromosomes. Chance matings between the two classes of sperm and the eggs (all alike) give the results shown in the following scheme.

Sperm.		Egg.	Individual.
X	→	X	XX female.
or			
O	→	X	XO male.

The egg that is fertilized by a sperm containing the accessory produces a female; the egg fertilized by a sperm without the accessory produces a male.

In a few insects, as in *Tenebrio,* the X-chromosome has a smaller chromosome for its mate, as shown by Stevens. This has been called by Wilson the Y-chromosome. Two classes of sperm are produced with an equal number of chromosomes, but in one class the X-element is present, and in the other its smaller mate the Y-chromosome.

All of the eggs of *Tenebrio* have two X's, one of which is lost in the polar body, so that only one remains, the egg that is fertilized by a sperm bearing the X-chromosome produces a female, the egg fertilized by the sperm bearing the Y-chromosome produces a male. The following scheme shows the results graphically.

Sperm.	Egg.	Individual.
X	X	XX female.
or		
Y	X	XY male.

In a third class of insects the X-chromosome has a mate of equal size; consequently all of the sperm, have the same number of chromosomes of the same sizes. Since we can not here distinguish X from Y, we may assume either that Y is the same as X, in which case we should have the problem of the four X's; or we may assume that despite their similarity in size they are nevertheless qualitatively different. In this case we should still speak of one of them as Y, and imagine that when a sperm bearing a Y enters an egg a male results. In favor of the latter interpretation Wilson has pointed out that an unbroken series of forms exists at one end of which the X-chromosome has no partner, in the middle of the series a partner of unequal size, toward the other end of the series a partner of nearly equal size, and at the end of the series a partner of equal size. If we are justified in attributing the male sex to no X, or to Y, it may seem that when Y can no longer be distinguished by its size it may still be responsible for the production of maleness. On the other hand, if X and Y do not in themselves produce sex, but simply accompany more profound changes, they are only indices of what is taking place and the graded series has no important significance.

These cases all apply to the group of insects. The criticism has been made that we are not justified in extending these conclusions to other groups where no such difference in number of chromosomes exist.

Quite recently surprising results have been obtained in groups other than the insects, that go far toward meeting the criticism just referred to.

First Baltzer has found in the sea urchins that there are specific chromosomes found only in the female. The *spermatozoa* are all alike, but the *eggs* are of two classes. In principle the outcome is the same except in so far as it shows that the sex element may be confined either to the male or to the female. Second, Guyer has found in the fowl that there is an odd chromosome in the male. This is the first case reported for the vertebrates, but the chromosomes in the group are so numerous or the cells so small that failure to detect two classes of sperm in this group (if they exist) is not surprising. Lastly, the all-important outstanding case of *Ascaris* has been brought into line by the announcement within the last few weeks by Boveri of the discovery of an accessory in this group.

In one of the nematode worms of the pheasant he has found that there are two classes of sperm, one with one more chromosomes than the other. Correspondingly, there are two kinds of embryo, male and female, differing by one chromosome in every cell.

In the classic case of the nematode of the horse, *Ascaris megalocephala,* the reduced number of chromosomes is *one* in one variety and two in another, it has been found by one of Boveri's students that about half the embryos contain one more chromosome than the other half. This chromosome is attached to one of the others in the early stage and hence does not appear as single.

This discovery shows that even when no accessory is found it may still be a part of one of the other chromosomes—and being confined to one sex fulfills all the conditions of the sex mechanism.

The conclusions arrived at from a study of these unisexual animals have been confirmed in the parthenogenetic phylloxerans and aphids.

Two years ago I found that in the phylloxerans two classes of spermatozoa are present; *one* is a rudimentary sperm, and corresponds to the male-producing of other insects. The other sperm contains the accessory, and it alone is functional. Hence all the fertilized eggs should be female. This has been known for a long time to be the case.

The female is the stem-mother of the summer brood of parthenogenetic individuals. They all contain the full number of chromosomes and are females. At the time when males appear a peculiar process occurs. When the male egg gives off its single polar body one (or two) whole chromosomes lag behind the others (that divide) and are thrown out into the polar body. Hence this egg contains two less chromosomes and it develops into the male. In the sexual female no such reduction takes place.

Here then we find a mechanism in the male to produce only females, but also another mechanism in the parthenogenetic female for producing males. The facts make out a strong case in favor of the view that we have probably found the mechanism by means of which sex is determined.

When we try to analyze the results, however, I mean when we try to make clear to ourselves how the accessory determines sex, we fail to make good a consistent story of the process.

If we assume, as Wilson and I have done, that the result is purely *quantitative* in that the *female* develops because the egg fertilized by the female producing sperm contains one more chromosome than the egg that becomes a male; when we make this assumption, we seem to leave unexplained how sex is determined in a large number of cases when the odd chromosome has a partner of equal size.

On the other hand, if we assume that the accessory is a *qualitative* agent producing females in this way; then the mate of the accessory, or one of the corresponding chromosomes in the female, must be male-producing. To make this mechanism "go" we must assume *selective* fertilization; for which at present there is no evidence.

I shall try to indicate in the barest outline the further analysis of the two statements just made.

When the accessory has no mate, as in the examples just given, we have the problem of the three X-chromosomes. The following situation then develops.

(A) The three X's are identical as everything we know about them indicates. Their position on the reduction spindle both in the male and female is so far as we know fortuitous. It follows then the female results when two X's meet in the same egg, and a male when only one X is present. This is the simplest explanation yet found that is strictly in conformity with observed relations for this class. It encounters five difficulties: first, it does not seem to apply when the accessory has a mate of equal size, if that mate be another X (see below); second, sex in hermaphroditic forms is not apparent on this view; third, the mate of the accessory when it exists, if it is not an X but a Y element, is ignored; fourth, in *Acholla* the Y element is larger than the combined X elements all taken together; fifth, it may seem to reduce the male to a less highly developed form than the female in the sense that it lacks a quantitative factor and leaves unexplained the characters peculiar to the male.

(B) If the three X's are not identical, but consist of two female and one male element, and if they are undirected on the spindle, the results can be explained only by assuming selective fertilization. The assumption meets with a flat contradiction in that it must assume that the only X in the male is a female X. Were it assumed to be a male X, the scheme will not work out. Moreover, there is no evidence for selective fertilization.

(C) If the three X's are not identical, but male and female, and are directed on the maturation spindles, equality of males and females will result only on the assumption of selective fertilization. Three assumptions, all unknown, are necessary to work out this scheme.

Let us turn our attention to the class with three X's and one Y. I take the simplest case for analysis in which all three X's are assumed to be alike. The sperm, bearing the X, fertilizing any egg (for all eggs have an X), produces a female, the sperm bearing the Y fertilizing any egg produces a male. We know this, in fact, to happen whenever we can identify Y. This scheme meets with no difficulties on its own account, and appeals (with certain modifications) more directly to my mind than any other; but it meets with a difficulty when no Y is present; and also when Y is the same size as X, if this size relation identifies Y with X. Unless these points can be met the hypothesis is insufficient to meet the situation. I shall return to these difficulties in a moment and try to meet them. This is the extreme application of the particulate theory, and has the advantages and disadvantages of its kind.

On the other hand, there is no need to assume that X is the *sex chromosome* in the sense of carrying sex. The use of this term, I fear, prejudices the situation by the very aptness of the application. It may be that X only means more X, and that this is a factor in sex determination. The only criticism that I have to offer of this view is that it ignores the Y element, and thereby makes the male condition the result of the absence of something which, if present, turns the embryo into a female. It seems to me that there is no warrant for considering the male in this sense a lacking female. The physiology and the biology of the males offer much to contradict such a view of his composition. I should also object to the above conclusion on the general grounds that it refers a particular character to a single chromosome.

Can we meet these objections if we admit that when the Y chromosome is absent the things that it stands for are redistributed, or are present in the other chromosomes whether equally or unequally distributed there need not be decided? Correspondingly, the materials of the X chromosome may be supposed to be distributed in part also to the other chromosomes. The production of male or female will then be determined by the preponderance of the amount of X or of Y in any given combination.

The groups with an accessory represent from this point of view an extreme form of distribution of the X material; while those with a Y show a like distribution of the Y material, but in neither case need we imagine all of this material present in a given chromosome, *i. e.*, in X or in Y. But this assumption also meets with difficulties in another direction, for we should be obliged to assume that the chromosomes carrying the Y element pass to the opposite pole at one division from those bearing the X element and we have as yet no evidence to support such a view.

These are some of the difficulties of interpretation:

Science advances by carefully weighing all of the evidence at her command. When a decision is not warranted by the facts, experience teaches that it is wise to suspend judgment, until the evidence can be put to further test. This is the position we are in to-day concerning the interpretation of the mechanism that we have found by means of which sex is determined. I could, by ignoring the difficulties and by emphasizing the important discoveries that have been made, have implied that the problem of sex determination has been solved. I have tried rather to weigh the evidence, as it stands, in the spirit of the judge rather than in that of the advocate. One point at least I hope to have made evident, that we have discovered in the microscopic study of the germ cells a mechanism that is connected in some way with sex determination; and I have tried to show, also, that this mechanism accords precisely with that the experimental results seem to call for. The old view that sex is determined by external conditions is entirely disproven, and we have discovered an internal mechanism by means of which the equality of the sexes where equality exists is attained. We see how the results are automatically reached even if we can not entirely understand the details of the process. These discoveries mark a distinct advance in our study of this difficult problem.

SPIEGLER'S "WHITE MELANIN" AS RELATED TO DOMINANT OR RECESSIVE WHITE[1]

DR. ROSS AIKEN GORTNER

STATION FOR EXPERIMENTAL EVOLUTION, COLD SPRING HARBOR, N. Y.

INTRODUCTION

THE study of melanin has interested a great number of chemists during the last century and of especial interest was the announcement by Spiegler,[2] in 1904, that he had succeeded in obtaining a "white melanin" from sheep's wool and white horse hair.

The question of white plumage and hair color has been widely studied from breeding standpoints—attracting unusual interest from the fact that there are undoubtedly two varieties of white, one of which is dominant and the other recessive. The reason for this peculiarity seemed, therefore, to be explained by the discovery of the "white melanin." In the light of this new knowledge it would seem that one variety of white was produced by the presence of a white coloring matter and that this would be dominant in a cross with another color having a weaker determiner. The recessive white, however, would be recessive because there would be an entire absence of pigment and would therefore be a case of dominance of color over absence of color.

Riddle,[3] in referring to Spiegler's work, seems to take this view, as does also Spillman.[4] Spiegler,[5] in a later paper, while giving no further experimental work on

---

[1] Used in the Mendelian sense. [Contribution from the Biochemical Laboratory of the Station for Experimental Evolution, The Carnegie Institution of Washington.]

[2] Spiegler, Hofmeister's *Beitr. z. Chem. Physiol. u. Path.*, 4, 40, 1904.

[3] Riddle, *Biol. Bull.*, 16, 328, 1909.

[4] Spillman, this journal, 44, 119, 1910.

[5] Spiegler, Hofmeister's *Beitr. z. Chem. Physiol. u. Path.*, 10, 253, 1907.

"white melanin" seems also to suggest that the two whites are due to the presence and absence of melanin. He states:

> It is readily understandable that white horse hair can not be without pigment. We know pigmentless hair, *i. e.,* albinos, these have apparently the natural color of the keratin (Hornrohstoffs) from which the hair is formed, modified by a special morphological condition. These questions need a more searching study. We must now determine whether albino hair gives the same oxidation products as pigmented hair. It is in this manner that we can finally decide whether the color of gray hair is due, as we have previously supposed, to disappearance of pigment and air content or rather to the change of the darker pigments into lighter ones.

It is in this condition that the study was left. Inasmuch as this question is of the utmost importance from the standpoint of heredity, the work of melanin investigation has been taken up in this laboratory.

In a study of Spiegler's[6] paper the most noteworthy detail which appears to be wanting is a comparison between the percentage of black pigment in the black wool or hair and the percentage of "white melanin" found in the white varieties. Spiegler gives the method of isolation as practically the same for both varieties, but does not mention the yields of melanin obtained. He, then, gives his analytical data leading to an empiric formula of $C_{50}H_{58}N_8SO_{12}$ calculated to ash-free (ash = 9.8 per cent.) melanin from black horse hair and $C_{45}H_{78}N_{10}SO_{20}$ calculated to ash-free (ash = 16.28 per cent.) "white melanin" from white horse hair.[7] He further states:

> The black pigment body with the simplest formula of $C_{50}H_{58}N_8SO_{12}$ and the light pigment body of $C_{45}H_{78}N_{10}SO_{20}$ differ, as the analytical data show *only a little* ("ein Geringes") *and it is very apparent that they are identical in nucleus* ("im Kerne"), and that the different color is due to the entrance of a chromatic group. Very apparent is the great difference in hydrogen content. The whlte pigment contains much more hydrogen, oxygen and even nitrogen, while the carbon-poor one is the black. The light pigment body is at the same time the oxidation and reduction product of the darker one.

---

[6] *Loc. cit.*

[7] His formula for melanin from black and white wool are respectively $C_{46}H_{68}N_8SO_{20}$ (ash = 10.85 per cent.) and $C_{61}H_{98}N_{10}SO_{20}$ (ash = 2.30 per cent.).

In other places, however, he prefers to call the white body an *oxidized black pigment.* In his paper no comparison is made of the black and white wool products; here we have formulæ assigned by Spiegler as $C_{46}H_{68}N_8SO_{20}$ and $C_{61}H_{98}N_{10}SO_{20}$, respectively. In this case white *could not be an oxidized black,* neither does the lower carbon percentage belong to the black. It is incomprehensible to the author why Spiegler should assert that *"it is apparent that both are identical in nucleus."* The only point of identity which is *apparent* is that the same elements enter into the composition of each, but the proportions are so widely different that no close relationship seems possible. Coupling this with the facts that from black wool, treated in a manner very closely resembling Spiegler's method, the author has obtained 1.84 per cent. of black melanin, while from white wool only 0.06 per cent. of a grayish-brown[8] body was obtained by an exactly similar method; and also that albino hair (from white rabbits), obtained through the courtesy of Dr. Castle of Harvard College, gave 0.03 per cent. of a grayish-brown body; feathers from a recessive (albino) fowl (silky) gave 0.155 per cent. of a similar body and feathers from a dominant white fowl (white Leghorn) gave 0.195 per cent., it appears that Spiegler's "white melanin" is not a substance belonging to the melanin class, but is a product produced from the keratin by the action of alkalies. The author has been able to find no data as to the actual percentage of keratin in the hair or feathers of the various animals, but it seems probable that the coarser the covering of the animal, the greater the percentage of keratin. Thus in the fowls we find the coarse ribs of the feathers, which are composed almost wholly of keratin, while in the white rabbit the hair is very fine and silky and contains, supposedly, less keratin than the intermediate wool of sheep, which is more similar to the rabbit hair. The same holds true of the decomposition product found if we assume it is due to the keratin—the coarser the structure of the coat the larger was the percentage of the decomposition product. Even if this view is not correct we know that the various keratins do not have the same composition,[9] and, therefore, we should look for a variation in any one decomposition product.

---

[8] Spiegler describes his "pigment" as "a light gray brown powder."

METHOD OF ISOLATION

A weight of wool was boiled with a 10-per-cent. solution of sodium hydrate[10] in the proportion of 300 grams to 1 liter for four hours. The solution was then poured into water, strongly acidified with hydrochloric acid[11] and the precipitate allowed to settle. The supernatant liquid was syphoned off and the precipitate washed by decantation. The precipitate was then stirred with from 5 to 10 liters of 0.2-per-cent. sodium hydrate solution and filtered. The filtrate was precipitated by hydrochloric acid and allowed to settle, the liquid syphoned off and the precipitate dissolved in one liter 0.2-per-cent. sodium hydrate solution and again filtered, precipitated with hydrochloric acid, washed free of chlorides, dried at 100° and, lastly, extracted with carbon disulphide, alcohol and ether in Soxhlet apparatus, then dried at 105° and weighed.

DISCUSSION

From the table given below it can be seen that "white melanin" does not exist in either recessive or dominant whites, but that there is some product *formed by the decomposition of the keratin,* which behaves like a melanin, *i. e.,* is soluble in alkali and insoluble in acids or neutral solvents; perhaps this may be shown to belong to the melanin class, but it is at least common to all white plumage and hair.

---

[9] See Hoppe-Seiler's "Handbuch der Physiologisch und Pathologisch Chemischen Analyse," Berlin, 1909, pp. 518–519.

[10] An exhaustive research as to the effect of various strengths of sodium hydrate solution upon melanin is in progress in this laboratory, the details of which will soon be ready for publication.

[11] A copious evolution of hydrogen sulphide was observed in each case

The results obtained are given in the following table.

Substance.	Weight.	Vol. alkali.	Strength alkali.	"Pigment" found.	Per cent. found.
1. Black wool[12]	400 gr.	1340 c.c.	10%	7.35 gr.	1.84
2. White wool[13]	500	1675	10	0.30	0.06
3. " "[14]	500	1675	10	0.30	0.06
4. " rabbit hair[12]	100	350	10	0.03	0.03
5. Silky feathers[12]	110	350	10	0.17	0.155
6. " "	105	700	5	0.24	0.22
7. " "	95	3000	1	0.16	0.168
8. White leghorn feathers[13]	46	200	10	0.09	0.195
9. Cow's horn (colorless)	40	200	10	Lost before weighing, but present in appreciable amount.	

If the theory of v. Furth[15] is correct that melanin formation is the product of an oxydase acting upon an oxidizable chromogen, it would appear very probable that dominant whiteness is due to the presence of an inhibitory enzyme[16] in the epithelial cells which prevents the action of the oxydase, and that recessive whites differ by having neither the power to produce pigments, *i. e.,* lack of oxydase or chromogen, or both, nor do they possess the anti-oxydase which distinguishes the dominant whites. This being the case, the one type would be always dominant, *its determiner being the anti-enzyme,* and the other type (*i. e.,* albinos) would of necessity be recessive, inasmuch as, while they lack the power to produce pigment, they also are without means of inhibiting pigment production when the elements for its formation are present. Davenport[17] has already put forward a view very similar to the above and it is hoped that in the near future this laboratory will have sufficient data to test this hypothesis.

---

[12] Recessive in the Mendelian sense.

[13] Dominant in the Mendelian sense.

[14] Had been previously digested at 40° for 48 hours with 9 liters of 0.2-per-cent. hydrochloric acid containing 18 grams of pepsin (Merck's "scales" 1 to 3,000).

[15] v. Furth u. Schneider Hofmeister's *Beitr. z. Chem. Physiol. u. Path.,* 1, 229, 1902. v. Furth u. Jerusalem, *ibid.,* 10, 131, 1907.

[16] For the literature of the anti-enzymes see Vernon, "Intracellular Enzymes," London, 1908, pp. 208–211, and Kastle, "The Oxidases," Bull. No. 59, Hyg. Lab., U. S. Pub. Health and Mar.-Hosp. Serv., Wash., pp. 66 and 87, 1910.

SUMMARY

1. Dominant and recessive whites in the Mendelian sense, have no relation to the presence of Speigler's "white melanin."

2. The "white melanin" was found to be present in all forms of keratin structure which were studied, but in very small amounts as compared with true melanin from black wool.

3. In view of the small percentage of "white melanin" found, Spiegler's view that it is an "oxidized black" seems impossible; neither is this view upheld by a study of Spiegler's work.

4. It seems highly probable that Spiegler's "white melanin" bears no relation to true melanins, but is a decomposition product of the keratin.

5. A theory is advanced that dominant whites are due to the presence of an anti-oxydase which prevents pigment formation; recessive whites, on the other hand, have neither power to form pigments nor to inhibit the formation.

---

[17] Davenport, Report Am. Breeders' Assoc., 5, 382, 1909.

SHORTER ARTICLES AND CORRESPONDENCE

A PICKWICKIAN CONTRIBUTION TO OUR KNOWLEDGE OF WASPS.

To the Editor of the American Naturalist: It is very idle to criticize the critic, especially when he happens to be a personal friend! Still, I think the frequency of wasps' nests in Buckinghamshire is not part of the wide knowledge possessed by Dr. Raymond Pearl, or he would hardly suggest that queen wasps collected over nearly six square miles in the cottages of a Buckinghamshire rural district in the spring could by any conceivable probability be members of a *single* nest dispersed in the preceding autumn. Last year in the autumn I had taken for me upwards of fifty nests on the land of one small farm in the same county. Indeed, in the collection which Dr. Pearl considers might come from one nest, there were two or three races present, besides *Vespa vulgaris,* when the material was sorted out, conclusively demonstrating that if we obtained samples of relatively rare species we must be drawing from a very large number of nests. In fact, my guide in this matter—an entomologist with a very extensive knowledge of English wasps—writes of this collection, "I should not hesitate to regard them as a random lot."

Other nests are in hand, as well as population collections, but the main point brought out in the last paper, as in Dr. Warren's termite paper, is the fact that the variability of a population is almost *double* the variability within a single nest. Dr. Pearl as a "pure-linist" would find wasps an interesting study, although I fear that if he attempted to breed with the needful 100 to 200 nests, he might experience difficulties—and not only from the wasps! When he does so, I have little doubt that his experience and knowledge will enable him to replace by more solid data the "Pickwickian" contributions of the much-abused biometricians.

Karl Pearson.

Biometric Laboratory,
University College,
London, England,
May 20, 1910.

NOTES AND LITERATURE

HEREDITY

THE Fifth Report of the Evolution Committee of the Royal Society (London), like the preceding reports of this committee, is full of exceedingly interesting results of experimental work. Professor Bateson's committee is doing much to unravel the tangled thread of Mendelian inheritance. In the report in question I. B. J. Sollas gives the results of studies of color inheritance and of the inheritance of supernumerary mammæ in guinea pigs. The color factors recognized are:

G = factor for agouti ticking of the hairs.
B = factor for black pigment in eye and skin.
R = factor for red pigment in hair and red and chocolate pigment in eye and skin.
Ch = factor for chocolate pigment in hair, skin and eye.
C = factor for color.

Albinos with which he worked had colored points, hence in them the factor C was not absent, but either merely deficient or controlled in such a way as to confine color to the extremities.

The colored forms fall into two series—one black-eyed, the other ruby-eyed. In the series of black eyes we have the three color types agouti (GBRChC), black (BRChC) and red (BRC). In the ruby-eyed series we have cinnamon (GRChC), chocolate (RChC) and red (RC). The author is not entirely clear in the explanation of some of his formulæ. For instance, he offers no explanation why B does not occur in the hair of the red type in the black-eyed series. He does state, however, that in agoutis red spots occur because B fails to develop. Red spots occur also on black individuals for the same reason and on cinnamon individuals because of the failure of the chocolate pigment to develop. Each of the colors has one or more dilute forms.

The method of inheritance of supernumerary mammæ was not clearly made out. Several dwarf individuals occurred. Only one of these lived to maturity.

Miss Wheldale, in the same volume, gives further observations upon the inheritance of flower color in *Antirrhinum majus*. A chromogen (Y) allied to the flavone series of coloring matters appears to be the basis of color in these flowers. From this a yellow (xantheic) pigment arises which, when unmodified by ferments, gives rise to flowers with yellow lips, though the throat is ivory white. In some strains this yellow chromogen appears to be modified by a ferment (I) in such manner as to give flowers having both lips and throat ivory white (except for certain patches of yellow in the palate). An oxidase (L) acting on Y as modified by I gives a tinging of magenta color in the lips. L acting on Y in the absence of I gives crimson. A factor T, when present, causes the magenta color to extend from the lips into the tube. A factor D, probably also a ferment, deepens the shade of magenta, giving the color of the wild plant. D acts only in the presence of Y or I and L and T. Still another factor further intensifies the shade of color. Striping also occurs, the factor for striping being allelomorphic to D and recessive to it. There is also a concentration factor S. When S is homozygous the stripes are of an ivory background; when heterozygous the stripes are of a pale-colored background. Chemical studies indicate each of the color factors to be due to different definite compounds. An albino variety arises in the absence of Y. The albino is distinguishable from the ivory white.

Miss Marryatt, in the same volume, gives the results of the study of color inheritance in *Mirabilis Jalapa.* She finds a factor C for colored sap and a factor M which turns yellow sap red. One white strain was found to be lacking in both C and M. Another white strain had M but not C. The latter crossed with yellow gave red. The formula of the yellow strain was CCmm. The formula of the crimson strain was CCMM. Yellows heterozygote for C were paler in color than the corresponding homozygotes. Heterozygotes of the composition CcMM were magenta; those of the CCMm an orange-red, and CcMm magenta rose. The behavior of "flaking," a form of striping, was not fully made out.

Miss Wheldale also gives some very interesting results in another part of the report on the physiological interpretation of Mendelian factors for color in plants. White varieties of sweet peas and stocks were found to contain a colorless flavone (chromogen). Colored varieties are assumed to possess this chromogen in various stages of oxidation. Each shade of color appears, from chemical tests, to represent a distinct substance. Chemical studies of white and colored strains point to the following system of factors as the cause of color production: P is a peroxidase which sets oxygen free from X; X is a substance which functions as a peroxide; A is a ferment or oxidizer which reoxidizes X with atmospheric oxygen; C is a chromogen, the oxidation of which, by the combined action of A, X and P, gives anthocyanin. Additional factors, A_2, X_2 and P_2, similar in a general way to A, X and P, convert red into bluish-red and purple. Chemical tests indicate a shortage and not always entire absence of some of the above factors in white varieties. This bit of information is important in connection with the telеone theory recently proposed by the writer in an article in the AMERICAN NATURALIST, and accords with that theory.

Baur has recently published an extremely interesting report on his study of inheritance in *Antirrhinum*.[1] He gives some interesting details of methods with special reference to the avoidance of error in experimental work of this kind. He has found 22 unit characters, but deals with only 13 in this paper. Baur recognizes the following colors in *Antirrhinum:*

White = Miss Wheldale's white.

Yellow = Miss Wheldale's yellow.

Elfenbein = Miss Weldale's ivory. This differs from white by the presence of a pale-yellow chromogen, according to Miss Wheldale.

Rose-back; flesh-colored; chamois-rose; red; pale red; dark red; rubin.

The last six are superposed on yellow or ivory, and each of them may appear whole or as delilahs—that is, on lips only. The colors chamois-rose, red, dark red and rubin may also be striped (picturatum).

Baur recognizes the following color factors:

B (= Miss Wheldale's Y) is the basis of color.

bb is pure white, distinguished from ivory by absence of yellow in the throat.

B unmodified by other factors is yellow.

C in the absence of F (see below) converts B into elfenbein (ivory), and hence = Miss Wheldale's J.

F in the absence of R (see below) and in the presence of B causes a light rose color on the back of the flower, with a spot of similar shade on each side of the stem near the spur, giving Baur's rose-back type.

R with B and F gives flesh-color; but without B and F, R gives no effect.

M in the absence of A and the presence of B, F and R gives chamois-rose.

A in the presence of B, F, R and M gives red.

L in the presence of B, F, R, M and A, gives dark red. In the series of factors BFRMAL, each factor is dependent on all before it.

D spreads color from the lips over the tube. When D is absent all colored flowers have ivory or white tubes. D also makes the color of the lips more prominent. The factor D is independent of all previously mentioned factors.

G gives striping on colored ground.

---

[1] E. Baur, "Vererbungs- und Bastardierungs-Versuche mit *antirrhinum*," *Zeitsch. f. Ind. Abst.- u. Vererb.*, 1910, Bd. III, H. 1 u. 2, pp. 34–98.

O gives red veins on ground containing no red. This factor shows in the presence of B, R, F and C, and may belong in the series BFRMAL between R and M. This point is not yet determined.

Q with B, F, R and M gives a peculiar shining rose color. It probably belongs in the above series after M, but may be identical with L.

Another factor gives a faded appearance to the edge of the lower lip of red flowers. There also appears to be a factor that governs the width of the yellow spot on the lower lip of red flowers. Investigation of four other factors which appear to affect flower color is in progress.

The author thinks there are possibly 20 factors concerned in flower color in *Antirrhinum majus.* Several factors not yet fully investigated influence the size of the flower, the relative size of the two lips, etc.

In addition to factors affecting flower color the following were made out:

E. When this factor is missing the flowers are radial (peloric).

P. The absence of P gives a peloric form different from that caused by E.

Another factor when absent gives a split corolla different from the normal zygomorphic form.

An apetalous flower is also known, but its inheritance is not worked out.

All of the flower color factors, except perhaps the one for striping, affect leaf color. There are also other factors which affect the intensity of red in the leaves. Two affect the green color. The absence of one of them produced the chlorina type previously mentioned in these notes. The absence of the other produced the aureas, also previously mentioned, and which are intensely yellow-leaved, being unable to grow.

The number of factors which affect leaf form are, for the most part at least, identical with those affecting the flower form, but are not yet fully investigated. The factors affecting the habit of growth are not yet fully worked out. Some of them seem to be identical with some of the flower-color factors. One character has been found that certainly does not Mendelize. This is a variegation conditioned by the cytoplasm. Only three of the factors studied are completely dominant; the others are incompletely so.

Baur, in another paper,[2] presents some very interesting evidence in favor of the hypothesis that the so-called graft hybrids are periclinal chimeras, the surface tissue being that of one parent form, the underlying tissue that of the other parent. Examples of such hybrids are *Cytisus Adami, Crataegus-*

---

[2] *Ber. d. Deut. Bot. Gesellsch.,* Bd. XXVII, H. 10.

Mespilus graft hybrid, and H. Winkler's tomato-nightshade graft hybrid. The suggestion that the vegetative point of such forms consists of a more or less irregular mixture of the two tissues could hardly be true because one or the other tissue would soon gain the ascendency. Baur suggests that a careful study of mitosis in the vegetative point of such forms might settle the question.

East has recently published an interesting paper[3] dealing with the effect of selection on fluctuations. The conclusion is reached that neither the relative content of dry matter nor that of the nitrogenous matters of the potato can be changed by the selection of fluctuations and their subsequent asexual reproduction. In most potato fields there will occasionally be found plants which remain green after the main crop has matured and the vines died. East made a selection of plants maturing early and those maturing late, in some cases finding lateness or earliness reproduced in the selection, in others not. In one of these cases the long-lived plants selected from a variety were found to have pink sprouts, while a short-lived plant from the same variety had white sprouts. East suggests that either bud variation had taken place or that there had been an accidental mixing of two varieties.

There has been a good deal of work on selection for yield and other characteristics in old agricultural varieties, which indicate that bud variations or permanent mutations of one kind or another occasionally take place in such varieties, and that they gradually break up into a mixture of biotypes, which may differ in a considerable number of characteristics, including yielding power. Selection within such a variety might then result in the isolation of strains of better quality than the general average of the variety.

It seems to the writer that Dr. East has hardly given sufficient attention to the possibility of selection for improvement in old strains in which a considerable number of important mutations may have occurred. For instance, he says:

> As a result of these experiments I will not go so far as to say that variations in power of resisting physiological or fungus diseases do not occur in asexual reproduction, but I do believe that the relative probability that the commercial grower will obtain disease-resisting varieties by this means is negligible.

So far as newly isolated pure strains are concerned, the writer agrees very fully with this statement. There has, however, been a good deal of work which indicates that in old agricultural varieties variations have frequently occurred which render selection with a view to isolating the best strains present justifiable. Thus Waid, of the Ohio Experiment Station, Zavitz, of the Ontario Station, and L. G. Dodge, of the U. S. Department of Agriculture, have, by selection in old varieties of potatoes, obtained strains which outyielded the variety from which the selection was made. It is true the objection may here be urged that the supposed variety from which the selection was made was really a mixture, but this point is granted. The only question is as to how the mixture came about, whether by mutation or by mechanical mixture. It may not be possible to settle this question definitely because of the difficulty of proving the purity of an old variety; but the results that have been accomplished, it appears to the writer, do justify selection in old varieties with a view to isolating superior strains. After all, Dr. East would probably agree perfectly with the writer in what has just been said.

---

[3] E. M. East, "The Transmission of Variations in the Potato in Asexual Reproduction," Connecticut Experiment Station Report, 1909–10, pp. 119–160, plates 1–5.

Concerning the character of bud variations, a number of which were found in East's work, the author gives it as his opinion "that practically all, if not quite all, bud variations are losses of a dominant, or epistatic, character allowing the appearance of a recessive, or hypostatic, character." He mentions four pink or red varieties that produced white variations that were constant the next season; also a purple variety produced a similar white variation. Several apparent changes from white to colored tubers appear, but they were not hereditary, and the varieties producing such variations had pink sprouts. Two varieties are mentioned in which changes of shape from long to round tubers occurred, the changes being permanent. Several other similar changes occurred but were not permanent. Change from shallow to deep eyes occurred in four varieties. In one case a peculiar change in the habit of growth of the tuber occurred, the peculiarity consisting in the formation of two tubers on the same rootstock at some distance from each other. This occurred in several varieties, but in only one case was it hereditary. It is not known whether the new type is recessive or dominant, but in the bud variations above discussed the new types are all recessive. The author suggests that these bud variations "seem to show that Mendelian segregation is not limited to the reduction division in the maturation sexual cell." It does not seem to the writer that this is a necessary conclusion.

Bud variations would certainly arise if Mendelian segregation occurred in somatic division, but they would also occur if for any reason a dominant character should become latent. It certainly yet remains to be demonstrated that they arise from Mendelian segregation in somatic tissues.

Kastle has recently published a very important paper in which he summarizes the results of investigations relating to oxidases and related compounds.[4] The paper is too extensive to permit of an adequate review at the present time. It has, however, a very important bearing on many Mendelian phenomena, and those who are interested in this subject will enjoy reading this excellent bulletin.

Guyer has recently given us a very thoughtful paper[5] on the possible relation of the chromosomes to hereditary characters. His argument is directed specifically against the Weismannian hypothesis of determinants. He does not attempt to minimize the importance of the nucleus in ontogeny or in heredity, but he is inclined to regard the development of what we call hereditary characters as a result of interrelations between the nucleus and the cytoplasm.

Speaking of experiments in which fragments of protozoa containing various proportions of the nucleus regenerated the organism, he says:

> If the nucleus is an aggregate of qualitatively different morphological units, one would expect parts to be missing in the regenerative protozoa in proportion to the amount of nuclear matter removed, but the evidence does not bear this out. The regeneration is seemingly complete, only a longer time is required if but a small fragment of the nucleus is left in the piece.

These experiments on protozoa disprove the determinant theory as held by Weismann, de Vries and others.

Guyer points out that the bulk of the fertilized egg is cytoplasm of maternal origin and that the developing organism must therefore be more of maternal than paternal origin.

> Nevertheless, we can see how the veneer of individual traits may be equally of maternal and paternal origin if, to express it crudely, we look upon cytoplasm and chromatin, respectively, as responsive mechanism and inciting agent, the character of the response depending both upon the constitution of the cytoplasm and the materials (enzymes? nutritive substances?) emanating from the nucleus.

---

[4] J. K. Kastle, "The Oxidases," Hygienic Laboratory Bul. No. 59, December, 1909.

[5] M. F. Guyer, "Deficiencies of the Chromosome Theory of Heredity," University of Cincinnati, Series 2, Vol. V, No. 3, September–October, 1909.

For many years the writer has held the view that in so far as the chromosomes have a relation to hereditary characters the influence they exert results from the relation they hold to the nutritive processes. He is therefore prepared to accept Guyer's views as expressed above.

Guyer gives a very striking analogy for the possible part which cytoplasm and chromatin may play in the development of specific characters.

> Any one of several species of insects may produce galls on a given plant, but each kind of insect always produces its own specific type of gall. Here is an actual case of living protoplasm producing a specific character through the activity of its specific exciting agent—that is, the reaction between certain secretions of the insect and the living substance of the plant produces new and definite structures.

Change either factor and the resulting structure must be modified.

> Likewise in the germ cell, alterations in the constitution of either chromosome or cytoplasm must undoubtedly produce structural changes in the adult.

He further points out that the chromosomes may be looked upon as the greater source of variability because they are derived in much greater proportion from the two parents than is the cytoplasm.

Guyer intimates that changes first initiated in the chromatin might be reflected on to the cytoplasm from time to time and there conserved. While it would seem to be possible that changes in the chemical constitution of a chromatin body might effect changes in other chromatin bodies and in the cytoplasm, I see no reason why such an assumption is necessary to account for permanent and fundamental evolutionary changes. I think we may look upon the cytoplasm and each of the chromosomes as having more or less of an individual existence and that each of them may undergo evolutionary changes in constitution more or less independently of the others, though, as above pointed out, a change in one of these cell organs might initiate changes in others. We may look upon the organism at any time as merely an expression of the complex relations then existing between the cytoplasm and the chromosomes and between the various chromosomes themselves. These relations are disturbed by any fundamental change in the composition or metabolic activities of any of these cell organs. For instance, the dropping out of a chromosome might not only change quantitative relations between various metabolic activities, but it seems possible that at least some of the chromosomes may possess characteristics which would give rise to qualitative changes, in case the chromosome should drop out. I have pointed out elsewhere[6] that in order to explain Mendelian phenomena on the basis of the behavior of chromosomes in the reduction division, it is not necessary to assume in the chromosome definite pangenes or determinants as separate entities. Each chromosome may take part in all phases of development. It is hardly probable that any particular chromosome, with the possible exception of a few of them, possesses exclusively characteristics necessary to the continued existence of the race in which they occur. In other words, speaking in a general way, each of the chromosomes may possess all the metabolic powers necessary to the race, while at the same time each chromosome may differ from others in minor particulars, giving rise to such differences as we see in Mendelian character pairs.

The writer does not quite follow Guyer in doubting the adequacy of the above interpretation of Mendelian phenomena, because in a few instances inheritance of a different type has apparently been found, but he does agree with him when he says:

> There are no sufficient reasons, I think, why we may not look upon their (the chromosomes') differences as differences of mere elemental, chemical and physical constitution rather than as differences among systems of determinate morphological units. . . . Even in case of the divorcement of particular parental chromosomes in gametes . . . it would seem that we might account for the so-called Mendelian phenomena by attributing to the chromosomes simply chemical and physical differences without endowing them with morphological entities.

Guyer points out that because the three elements carbon, oxygen and hydrogen condition substances of which they are components, we do not postulate a specifically determinative substance in any of them for each of the numerous carbohydrates and other products that result from their various combinations and arrangements. Similarly, we do not need to infer definite structural elements in the chromosomes, each of which is specifically determinative of a given character. It would seem more logical to assume that the differences between related organisms may be due to differences in the combinations of metabolic activities found in the various cell organs.

This paper of Guyer's accords very closely with the teleone theory of heredity propounded by the writer in the April number of the American Naturalist, 1910. It is gratifying to see that a number of biologists are coming to the view that the main facts of heredity can be explained without the assumption of any hypothetical units in the germ plasm. W. J. Spillman.

---

[6] American Naturalist, April, 1910.

Methods in Plant Histology

By CHARLES J. CHAMBERLAIN

Second edition, revised and much enlarged; 272 pages, with 88 illustrations, 8vo, cloth; net $2.25, postpaid $2.39

THE first complete manual to be published on the subject of botanical microtechnique. It contains detailed directions for collecting and preparing plant material for microscopic investigation, setting forth the advantages and disadvantages of the different methods.

Will no doubt find a place in every well-regulated library, and will be found very useful by private students.—*Plant World.*

It is an excellent book for the individual worker and for classes in colleges.—*Education.*

A Laboratory Guide in Bacteriology

By PAUL G. HEINEMANN

158 pages, interleaved, with 37 illustrations, 12mo, cloth; net $1.50, postpaid $1.61

A CLEAR and concise presentation of bacteriological technique, designed principally as a manual for the medical student, but highly useful also as a reference book for the biological teacher and investigator, as well as for practical workers in the fields of medicine and hygiene.

The instruction given is clear and accurate, and the practical exercises are well selected.—*The Lancet* (London).

A book such as this must facilitate very greatly the practical class work, for which it is most excellently adapted. — *American Journal of Medical Sciences.*

The directions are clear and concise, and every stage is described so carefully that it is hard to see how the student can go astray. Physicians who are rusty in bacteriology cannot do better than buy this little book. The book is beautifully printed and bound.—*American Journal of Clinical Medicine.*

Animal Micrology:

Practical Exercises in Microscopical Methods

By MICHAEL F. GUYER

250 pages, 8vo, cloth; net $1.75, postpaid $1.88

THE title of this book will explain its scope. It is intended as a laboratory manual for textbook use. Its aim is to introduce the student to the technique of microscopic anatomy and embryology, emphasizing details of procedure rather than descriptions of reagents or apparatus. Sufficient account of the theoretical side of microscopy is given to enable the student to get satisfactory results from his microscope.

The directions are simple, explicit, and complete.—*American Journal of Clinical Medicine.*

The medical student will find it very useful as a guide to microscopic work.—*Journal of the American Medical Association.*

This is one of the cleanest works on microscopical technique we have ever seen, and is especially suitable for the beginner. It is full of points, tricks of technique not mentioned in other works, and is one that every student and physician should have.—*Medical Century.*

This valuable book is strong through its rigid exclusion of the trite and the conflicting. It is lucid and helpful, because a man long practiced in practical work has given what he believes the most expeditious and reliable method of obtaining a definite and comprehensive result. — *Medical Notes and Queries.*

A concise, eminently practical, and well-classified treatment.—*Science.*

The expositions of the methods recommended are admirably clear.—*Nature.*

One of the best and most practical works upon microscopic technique with which we are acquainted.—*American Naturalist.*

As a textbook it can hardly be improved. The research worker will find in this book just the information he frequently needs in preparing material with which he is not familiar.—*School Review.*

It does present in very clear form a judicious selection of methods, including an excellent untechnical account of the microscope and its optical principles, adequate for the undergraduate course in histology.— *Journal of Comparative Neurology and Psychology.*

ADDRESS DEPT. 64

Chicago THE UNIVERSITY OF CHICAGO PRESS New York

Cast of Head of Mummied Woman of the "Basket People" (Cliff Dwellers)

This is the specimen which Professor H. H. Wilder restored to approximately its normal contours by treating with a potash solution, as described in the American Anthropologist, Vol. 6, No. 1, Jan.-Mch., 1904.

The restored subject has been molded and cast in our laboratory. The head is tinted and is mounted upright on a black pedestal with incised label. Professor Harris writes:—"I have been out of town for a few days and on returning found what I consider a most successful rendering of my 'restored' Cliff Dweller lady, and wish to thank you heartily for attempting so difficult a task."

This head or bust is, perhaps, *the only authentic likeness of a prehistoric American in existence.* Copies, securely boxed, each.......................................$ 8.00

We can also supply the following casts, all colored after nature.

HOMO SAPIENS

Skull of Engis Man, restored portions indicated.......Price,	$2.00
Skull and Mandible of Cro-Magnon No. 1 (capacity much above the present average).......Price,	$4.00
Cranium of Cro-Magnon No. 2.......Price,	$3.00
Cranium of Australian.......Price,	$2.75
Cranium of Hottentot (recent).......Price,	$2.75
Series of brains of ten races of man (intercranial casts) from the Royal College of Surgeons. Casts are alabaster, coated with stearine. Each brain has its individual pedestal and label.......Price, set of ten,	$25.00

HOMO PRIMIGENIUS

Neanderthal Man, cranium and portions of skeleton (2 femora, 2 humeri, 1 radius, 2 ulnæ, 1 acetabulum, 1 scapula, 1 clavicle), together with intercranial cast.........Price, 12 pieces, $14, Skull or Brain, each,	$2.00
To facilitate the study of the anatomical peculiarities of this skull, a reprint of Professor Shaaffhausen's original description, now long out of print, is included.	
Man of Spy No. 1 includes calvarium, lower jaw, right sup. max., portions of clavicle and humerus, left radius, head of left ulna, right femur, and left tibia and patella.......Price,	$11.00
Man of Spy No. 2: Calvarium, portions of left femur, right humerus, radius ulna and tibia.......	$7.50
Skull only of Spy No. 1 or No. 2.......	$1.75
Cranium and mandible of Homo neanderthaloides, Pohlig, Brunn.......	$4.00
Brunn—Cranium No. 2.......	$3.00

PRE-HUMAN REMAINS

Mesopithecus pentelici, male cranium.......	$1.50
Mesopithecus pentelici, female cranium and mandible from the Pliocene, Pikermi, Greece.......	$2.00
Dryopithecus fontani, lower jaw on pedestal (Type-specimen of this large anthropoid from the fresh-water Miocene of Southern France).......	$2.25
Paedopithex rhenandus, femur, Pilocene, Eppelsheim, Germany.......	$1.25
Pithecanthropus erectus, cranium. Pliocene of Java.......	$3.00

An 8-page illustrated description by the late Professor Marsh accompanies this remarkable skull. We fill orders promptly.

ANATOMICAL LABORATORY OF CHARLES H. WARD

"THE LENNOX," WEST AVENUE ROCHESTER, N. Y.

VOL. XLIV, NO. 525 SEPTEMBER, 1910

THE
AMERICAN
NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. **Nuclear Phenomena of Sexual Reproduction in the Algæ. Dr. BRADLEY MOORE DAVIS** - - - - 513

II. **Nuclear Phenomena of Sexual Reproduction in Fungi. Professor R. A. HARPER** - - - - 533

III. **The Pose of the Sauropodous Dinosaurs. Dr. W. D. MATTHEW** - - - 547

IV. **Shorter Articles and Discussion:** Evolution without Isolation, Dr. JOHN T. GULICK. Retroactive Selection, CASPER L. REDFIELD. The Logic of Chance in Problems of Genetics, ARTHUR S. DEWING - - - - 561

V. **Notes and Literature:** Animal Structure and Habits, Professor G. H. PARKER. Plant Physiology, C. L. SHEAR - - - - 572

THE SCIENCE PRESS

LANCASTER, PA. **GARRISON, N. Y.**

NEW YORK: SUB-STATION 84

The American Naturalist

MSS intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

TO ORNITHOLOGISTS AND MUSEUMS

W. F. H. ROSENBERG

Importer of Exotic Zoological Specimens

57 Haverstock Hill, N.W., England

Begs to announce the publication of a new Price List (No. 11) of **Bird Skins**. This catalogue contains over 5,000 species, and is the largest and most complete price list of birds ever published. It is arranged in systematic order, based on the classification of the British Museum "Catalogue of Birds," with authors' names, indications of localities, and an index to families. It will be sent gratis and post free on application, as will the following lists: No. 7, Mammals; No. 8, Birds' Eggs; No. 9, Reptiles, Amphibia, and Fishes.

Largest stock in the world of specimens in all branches of Zoology.

Specimens sent on approval.

Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

Henry Holt & Company

34 West 33d St., New York

378 Wabash Ave., Chicago

Microscopes and Accessories

Hand Cameras of Highest Quality

Binoculars, Prism and Galilean

the best obtainable for Nature Study

Scientific Instruments

Laboratory Apparatus

Max Meyer 18 West 27th St. **New York**

"Quality, Prices, Service Right."

THE

AMERICAN NATURALIST

Vol. XLIV *September, 1910* No. 525

NUCLEAR PHENOMENA OF SEXUAL REPRODUCTION IN ALGÆ[1]

DR. BRADLEY MOORE DAVIS

Cambridge, Mass.

Cytological investigations among the algæ upon the processes of gametogenesis and the developments that follow upon the fusion of gametes have not been numerous and are all of comparatively recent date. The difficulties of obtaining and handling material in critical stages require great patience, but the importance of the problems has attracted attention to a field of enquiry in which considerable progress has already been made and which offers some of the most attractive problems for cytological investigation. There has been a very marked advance in our understanding of the Rhodophyceæ and Phæophyceæ, but the Chlorophyceæ have so far received little attention.

The advance has been chiefly in our interpretation of certain life histories in which complex developments follow upon the phase of sexual reproduction. The publication in 1894 of Strasburger's paper on "The Periodic Reduction of the Number of Chromosomes in the Life History of Living Organisms"[2] marked the beginning of that closer analysis of the life histories of the higher plants which presents the strongest support for the theory of antithetic alternation of generations. The higher plants were naturally the first which were subjected to critical cytological investigation and the structure and behavior of the nuclei through various stages of ontogeny have been studied in an increasing number of forms representative of the most important groups. Later came the pioneer work of this character upon the thallophytes which has given such rich returns in our appreciation of the significance of the critical stages in the complex life histories of certain types of the Ascomycetes, Uredineæ, Phæophyceæ and Rhodophyceæ.

---

[1] A paper read by invitation before the Botanical Society of America, Boston, December 30, 1909.

[2] *Ann. of Bot.*, Vol. VIII, p. 281, 1894.

It is the writer's part in this symposium to outline the advances that have been made in cytological research on the sexual reproduction of the algæ, and such enquiry, for a number of reasons, necessarily leads at once to the consideration of life histories with reference to cytological detail. From studies upon the bryophytes, pteridophytes and spermatophytes we have learned that in these groups every sexual nuclear fusion marks the beginning of a distinct phase in the life history, the sporophyte, the nuclei of which carry the double, or diploid, number of chromosomes characteristic of the species. Furthermore, we know that the sporophytic phase comes to an end with the numerical reduction of the chromosomes to the original, or haploid, number peculiar to the gametophyte. This significant period of chromosome reduction is associated in the bryophytes and pteridophytes with the formation of spores, in the spermatophytes with the formation of pollen grains and embryo sacs. Every sexual fusion, then, carries with it a prospective period of chromosome reduction.

Since such is the history for the higher plants we have every reason to expect that each sexual nuclear fusion among the thallophytes with the resulting doubling of the chromatin content in the zygote would be followed sooner or later by reduction phenomena. It becomes a matter of importance to determine when the latter event occurs, since between the time when the gametes fuse and that of chromosome reduction there is always the possibility of an intercalated sporophytic phase in the life history, the development of which will involve the mitoses of nuclei that carry twice the number of chromosomes characteristic of the sexual plant. From this point of view let us then consider in the order of the Chlorophyceæ, Phæophyceæ and Rhodophyceæ some of the recent cytological research which has made much clearer the significance of the life histories of certain important types.

There are in the life histories of a number of the green algæ certain outward signs that would lead one to suspect that the period of chromosome reduction in these forms takes place just previous to or during the germination of the zygospores or oospores. Thus the formation of several zoospores within the zygote of *Ulothrix* and *Hydrodictyon*, and of four zoospores in the oospore of *Œdogonium* at once excites suspicion that the first mitosis in these sexually formed cells is a reduction division. Still more striking is the phenomena described in the zygospores of the Conjugales where the fusion nucleus by two mitoses gives rise to four daughter nuclei, three of which in *Spirogyra* and two of which in the desmids *Closterium* and *Cosmarium* break down. Such behavior, involving a sacrifice of protoplasmic structure and energy, is not easily understood except that it be related to important events of ontogeny and phylogeny. Any one familiar with the cytology of spore formation in the higher plants or with oogenesis in animals would at once suspect that the zygospore of the Conjugales was the seat of reduction phenomena.

That this is really true has been shown by recent work of Karsten[3] who has followed the chromosomes of *Spirogyra jugalis* through the two mitoses within the zygospore. Karsten in agreement with Berghs reached the conclusion that the chromosomes in the resting nucleus of *Spirogyra* lie in the substance of the large nucleole.[4] He was able by the proper extraction of stain to differentiate fourteen bodies in the gamete nucleus which corresponded in number to the fourteen chromosomes that may be readily counted for this species in later mitoses. The union of the gamete nuclei in the zygospore involves the fusion of the two nucleoles to form a dense homogeneous structure in preparation for a characteristic association of the two sets of chromosomes, one derived from each parent.

---

[3] Karsten, G., 1908, "Die Entwicklung der Zygoten von *Spirogyra jugalis* Ktzg.," *Flora*, Vol. XCIX, p. 1, 1908.

The approach of the first mitosis is indicated by changes within the fusion nucleole where a granular structure begins to appear, accompanied by irregularities in its form. As these changes proceed an assemblage of deeply staining bodies becomes evident which in later stages are readily identified as chromosomes. There are twenty-eight of these grouped in fourteen pairs, an arrangement which is characteristic of a phase of chromosome reduction that follows synapsis and which signifies that the chromosomes are to be distributed in two sets of equal numbers by the following mitosis. This distribution occurs in *Spirogyra* and the second mitosis in the zygospore is concerned with the reduced, or haploid, number of chromosomes. Thus the double, or diploid, number is present only in the fusion nucleus; the numerical reduction takes place with the first mitosis. There are no nuclear divisions in which the diploid number of chromosomes is passed on, and assuming that the sporophyte generation is characterized by nuclear divisions with the diploid number of chromosomes, there is no sporophytic phase in this life history.

So close is the parallelism between the events of reduction in *Spirogyra* and those of higher plants that Karsten even reports evidence for the premature division of the chromosomes during the first mitosis in preparation for the second division, a phenomenon very characteristic of the reduction divisions of higher plants. The degeneration of three of the four nuclei which result from the two mitoses within the zygospore of *Spirogyra* is of course an illustration of that conservation of material for a single reproductive cell which finds its analogy in the history of development of certain megaspores at the expense of their neighbors and in the maturation of the animal egg.

---

[4] B. F. Lutman has, however, recently reported (*Science*, Vol. XXXI, p. 633, 1910) that the chromosomes of *Closterium* are formed from a spirem which has its origin in the fine reticulum around the nucleole.

It seems probable that studies upon the germinating zygospores and oospores of other green algæ will establish them to be the seat of reduction phenomena similar to that described above, although such investigations are beset with many technical difficulties. It is to be hoped that we may soon have information on these conditions in such types as *Œdogonium, Sphæroplea, Chara* and *Vaucheria.* The complexities reported in the formation of auxospores among the diatoms take on new interest in relation to the conditions in *Spirogyra.* In none of these forms have we at present any reason to expect the presence of a sporophytic generation.

Coleochæte has long been regarded as a type of peculiar interest chiefly perhaps because its oospore on germination gives rise to a small group of cells, each of which develops a zoospore. It is not strange that this cellular structure, a phase intercalated between two sexual plants, should have been compared with the simplest types of sporophytes in the liverworts, and that in attempts to bridge the gap between the thallophytes and bryophytes *Coleochæte* should have been brought forward as illustrating the primitive beginnings of a sporophyte generation.

A cytological study by Allen[5] on the germination of the oospore of *Coleochæte,* however, presents evidence that the first mitosis in the oospore is a reduction division and that consequently the later mitoses can not be sporophytic in character. Allen found that when the fusion nucleus made preparations for the first mitosis the chromatic material previously in the form of an irregular network gathered at one side of the nucleus in the manner characteristic of synapsis. There was evidence of a pairing of the chromatic threads during the process of synapsis which is interpreted by this author as indicating a pairing of the chromosomes from the two gamete nuclei. Following synapsis the chromatic material becomes distributed as a coiled thread from which the chromosomes are differentiated, that in a later stage are found scattered through the nuclear cavity. A count of the chromosomes at this stage indicated that the number thirty-two is the double or diploid number for the species studied. Some of the chromosomes were clearly associated in pairs, a condition that becomes more evident in later stages when at metaphase of the first mitosis the now much condensed chromosomes are assembled at the equatorial plate. In this mitosis the chromosomes are short and thick, in sharp contrast to the long narrow bent rods which are characteristic of the second mitosis. Allen then bases his conclusion that the first mitosis in the oospore is a reduction division chiefly on the presence of a stage similar to synapsis preceded by a long resting period, and on peculiarities in the form and grouping of the chromosomes, which peculiarities are similar to those of the heterotypic division in higher plants.

---

[5] Allen, C. E., 1905, "Die Keimung der Zygote bei *Coleochæte,*" *Ber. deut. bot. Gesell.,* Vol. XXIII, p. 286, 1905.

It would seem then that *Coleochæte* can no longer be considered as a type very helpful in considerations of the origin of the sporophyte or suggestive of affinities with the archegoniates. With respect to the latter point the simple unicellular character of the sexual organs offers further difficulties to a relationship to the archegoniates, since the multicellular archegonia and antheridia of this last group apparently require an origin from a multicellular type of sexual organ such as is best illustrated among living forms by the plurilocular sporangia and gametangia of the Phaeophyceae. The writer has discussed this problem in a paper on "The Origin of the Archegonium,"[6] and advanced the view that the archegonium and antheridium arose from some type of plurilocular sporangium or gametangium through the differentiation, in response to terrestrial life habits, of a sterile protective envelope around the gametes. Schenck in a contribution "Ueber die Phylogenie der Archegoniaten und der Characeen"[7] accepts the above view and even argues for a direct descent of the archegoniates from the Phæophyceæ, carrying the speculation far beyond the point with which the writer is in agreement. A discussion of the difficulties which face Schenck's hypothesis would, however, lie outside of the province of this paper.[8]

Assuming that the sporophyte is normally characterized by mitoses concerned with the diploid number of chromosomes, the results of the recent research on the Chlorophyceæ make it appear probable that none of the known living types present an alternation of generations even in its simplest form. The striking differences between the Chlorophyceæ and the simplest archegoniates have become more strongly emphasized by the latest research.

Passing to the Phæophyceæ we shall have to consider cytological conditions and life histories very much more complicated than any that are known for the Chlorophyceæ. Only the specialist among the algæ can fully appreciate the diversity of the types and lines of development in the large assemblage of forms termed the brown algæ. The chief groups exhibit greater differences among themselves than do the divergent lines among the green algæ. Unfortunately our information on the cytology of reproduction in the Phæophyceæ is limited to three groups, the Dictyotales, Fucales and Cutleriaceæ, groups which occupy isolated positions of problematical relationship to the lower forms of the Phæophyceæ.

---

[6] *Ann. of Bot.*, Vol. LXVII, p. 477, 1903.

[7] *Engler's Botan. Jahrbücher*, Vol. XLII, 1908.

[8] See review by Davis, AMER. NAT., Vol. XLIII, p. 107, 1909.

We have from the investigations of Williams[9] an account of the cytology of *Dictyota* throughout the critical phases of its life history. There are three forms of this alga, the male and female sexual plants and an asexual plant which develops spores in groups of four (tetrads) within a tetrasporangium. Earlier research of Mottier indicated clearly that the tetraspore mother-cell is the seat of chromosome reduction, and Williams by studies of the sexual plants as well as the asexual was able to present convincing cytological evidence of an alternation of generations.

Williams found that the sexual plants were characterized by nuclei with sixteen chromosomes and that this number was passed on to the eggs and sperms respectively. Fertilization takes place following the discharge of the gametes, which have the peculiarity of being developed in fortnightly crops, "each crop being initiated a little before the lowest neap tide, and arriving at maturity about the period of the highest succeeding spring tide". The motile sperms gather about the eggs which for a short time exert a strong chemotactic influence. Following the union of the gamete nuclei, a second nucleole appears in the fusion nucleus which Williams believes to be the chromatin brought by the sperm. The first mitosis in the egg presents thirty-two chromosomes at the equatorial plate, and this is believed to be the first mitosis of a sporophyte generation represented by the asexual plant and terminating with the development of the tetraspores.

The spindle poles of the first mitosis in the eggs appear to arise by the division of an aster the two poles of which separate until they come to lie on opposite sides of the nucleus. It is an interesting fact that unfertilized eggs begin a parthenogenetic development, but the spindles of the first mitosis are multipolar and the chromosomes are distributed irregularly to a cluster of small nuclei. It would seem then either that the sperm brings to the egg a directive element in the form of an aster, which gives polarity to the fusion nucleus, or that in the absence of fertilization the egg is unable to develop the mechanism necessary for a normal mitosis.

---

[9] Williams, J. Lloyd, 1904, "Studies on the *Dictyotaceæ*." I., "The Cytology of the Tetrasporangium and the Germinating Tetraspore," *Ann. of Bot.*, Vol. XVIII, p. 141, 1904. II., "The Cytology of the Gametophyte Generation," *Ann. of Bot.*, Vol. XVIII, p. 183, 1904.

It is the purpose of this paper to consider the nuclear phenomena of sexual reproduction among the algæ in the broadest sense, and this must involve the consideration of any sporophytic generation when present. It has become clearly established by the cytological research of recent years that the sporophytic phase in a life history is a period during which one of the final ends of a sexual nuclear fusion, the intimate association of the sets of parental chromosomes, is delayed and in consequence the mitoses of this period deal with double the number of chromosomes present in the sexual plants. Williams found in the case of *Dictyota* that the mitosis which cuts off the tetraspore mother-cell presented the same large number of chromosomes as the first division of the egg, *i. e.*, twice the number characteristic of the sexual plants. The inference is clear that the vegetative mitoses throughout the development of the asexual plant must be sporophytic in character, and that this generation must have developed from the fertilized egg.

With respect to the two mitoses within the tetrasporangium, the main events are evidently those characteristic of a numerical reduction of the chromosomes. There is a stage of synapsis in which a long thin spirem is found closely coiled in knots against the nuclear membrane. Following this comes a loosening up of the spirem and the differentiation of sixteen chromosomes, the reduced number. The form of the chromosomes, which are loops and closed rings, indicates at once to one familiar with the peculiarities of the heterotypic mitosis that these structures are really pairs of sporophytic chromosomes (bivalent chromosomes) in close association.

The members of each pair are separated by the first mitosis which thus distributes the thirty-two chromosomes in two sets. The second mitosis (homotypic) presents sixteen simple chromosomes in the form of bent rods, similar to those found in the gametophytes. The cytological evidence justifies the conclusion that the tetraspores give rise to the sexual plants and that the fertilized egg must develop the asexual plant, and thus is established an alternation of generations.[10]

The peculiarities of the life history of *Fucus* in relation to the life histories of plants in general are most striking. It became evident from the studies of Strasburger in 1897 and of Farmer and Williams in 1896–98 that the mitoses within the oogonium presented only half the number of chromosomes which were present in the vegetative cells of the Fucus plant. This placed the period of chromosome reduction just previous to the differentiation of the gametes, a condition that is not known in any other group of the thallophytes. To bring such a life history into relation with the prevailing conditions in the lower plants becomes a most interesting problem of plant morphology and phylogeny.

We have recently had from Yamanouchi[11] a much more detailed account of the reduction processes in *Fucus* than the descriptions of the earlier writers. The nucleus within the young oogonium passes through a remarkably clearly defined stage of synapsis during which chromatic threads, derived from a reticulum, become arranged in loops that are gathered together closely attached at one side of nuclear membrane. Close to this point but outside of the nuclear membrane, there is developed an accumulation of kinoplasm from which is differentiated an aster with a chromosome, so that the nucleus during synapsis exhibits strongly marked polarity.

---

[10] Since the above was written W. D. Hoyt (*Bot. Gaz.*, Vol. XLIX, p. 55, 1910) has announced his success in raising from the fertilized eggs of *Dictyota dichotoma* fruiting plants which proved to be asexual (tetrasporic) and from the tetraspores sexual plants both male and female. Thus the conclusions based upon cytological evidence have been sustained by cultural studies. Such investigations are especially difficult to conduct in the case of marine algæ, but it is to be hoped that Hoyt's success with *Dictyota* will lead to further studies of this character, especially upon forms of the Rhodophyceæ.

[11] Yamanouchi, S., 1909, "Mitosis in *Fucus*," *Bot. Gaz.*, Vol. XLVII, p. 173, 1909.

The chromatic loops extend into the nuclear cavity and sections show them to be thirty-two in number. After a period of condensation each loop is transformed into a pair of chromosomes by the separation of the arms at the bend. The pairs of chromosomes then become scattered through the nuclear cavity (diakinesis). The interpretation of this history is that the sixty-four somatic chromosomes of the *Fucus* plant are arranged end to end on the spirem and become associated in thirty-two pairs through the formation of the loops. Meanwhile a second aster appears, apparently arising *de novo,* generally at some distance from the first, and the two asters establish the poles of the first spindle. The thirty-two pairs of chromosomes are gathered at the equatorial plate and the members of the pairs distributed in two sets, thus affecting a numerical reduction by one half of the sixty-four somatic chromosomes.

There is apparently no premature division of the chromosomes in preparation for the succeeding division, as is generally the case in the heterotypic mitosis. The second and third divisions in the oogonium are similar in all essentials to typical mitoses. They deal, of course, with thirty-two chromosomes, the haploid number, which divide lengthwise during the metaphase of each mitosis. There is a long period of rest following the second mitosis. The first mitosis in the antheridium is likewise a reduction division similar to that in the oogonium and need not be described in this connection.

The nucleus of the unfertilized egg exhibits no evidence of polarity, but following the entrance of the sperm, according to Yamanouchi, an aster with a centrosome becomes at once evident. A second centrosome with radiations appears later at the point where the sperm fuses with the egg nucleus. These two asters establish the spindle poles of the first mitosis, which presents sixty-four chromosomes. The chromatin of the two gametes is indistinguishable in the fusion nucleus.

The interpretation of the life history of *Fucus* with its phase of chromosome reduction so close to the differentiation of the gametes involves great difficulties. Strasburger has long held the thallus of this plant to be a sporophyte generation, assuming that the gametophyte phase is represented by the third mitosis in the oogonium and the few antheridial mitoses which follow the reduction division. He would then regard the antheridia and oogonia to be derived not from primitive sexual organs, but from sporangia corresponding to the tetrasporangia of *Dictyota*. This view involves a reversal of the relations between the gametophyte and sporophyte generations usual among the algæ, since it supposes the almost complete suppression of the gametophyte. However interesting and suggestive is this interpretation, it can hardly be considered other than a speculation until we know more of the probable phylogeny of the *Fucales*.

It has been evident for a number of years that the life history of the Cutleriaceæ probably involved two phases represented by sexual and asexual plants, respectively, and there has accumulated much evidence from the studies of Reinke, Falkenberg, Sauvageau, Church and others indicating that these phases present a true alternation of generations. The forms most studied have been *Cutleria multifida* with a large much branched thallus which develops gametes, and *Aglaozonia reptans*, a small crustaceous alga which reproduces by zoospores. On the germination of the zygotes and zoospores of these types forms are produced which very shortly take on vegetative characters not of the parent plants, but from the zygotes arise *Aglaozonia*-like sporelings and from the zoospores sporelings totally unlike *Aglaozonia*, but with characteristics of *Cutleria*. Upon this behavior chiefly have been based the suggestions of an alternation of generations in the Cutleriaceæ.

A preliminary paper by Yamanouchi[12] on the above named species presents cytological evidence in support of the theory that they are sexual and asexual phases, respectively, of the same life history, with the relation one to the other of gametophyte and sporophyte. The vegetative mitoses of *Cutleria multifida* and those leading to the formation of the male and female gametes show uniformly twenty-four chromosomes. The zygote develops at once into a sporeling, the nuclei of which have forty-eight chromosomes. There is thus no reduction of the chromosomes at the time of the germination of the zygote, and the sporeling which results must be considered as sporophytic in character.

The vegetative mitoses of *Aglaozonia reptans* exhibits forty-eight chromosomes, but the nuclear divisions within the sporangia are quite different. Following the differentiation of a sporangium, the nucleus passes through a stage of synapsis in which the chromatic spirem is arranged in a series of loops from which are developed twenty-four bivalent chromosomes. The first division in the sporangium is therefore a heterotypic mitosis. Later mitoses in this cell exhibit the reduced number of chromosomes. Since sporogenesis in *Aglaozonia* is accompanied by reduction phenomena, there must be in its life history a sexual phase of which it is the sporophyte generation, and the number of chromosomes as well as other details of cell structure present strong cytological evidence that the gametophyte is *Cutleria*. Such evidence supporting the conclusions of the earlier writers based on the seasonal habits of *Cutleria multifida* and *Aglaozonia reptans* and on the structure of the respective sporelings, makes as strong a case for an alternation of generations in the Cutleriaceæ as is possible short of the actual cultivation of these algæ from zygotes and zoospores to fruiting maturity.

---

[12] Yamanouchi, S., 1909, "Cytology of *Cutleria* and *Aglaozonia*," *Bot. Gaz.*, Vol. XLVIII, p. 380, 1909.

These results from studies on the three most highly differentiated groups of the Phæophyceæ (Dictyotales, Fucales and Cutleriaceæ) indicate how complex has been the evolutionary history of the divergent phyla assembled under this name, and how difficult are likely to be the problems of tracing their relationship to lower groups of the brown algæ.

Perhaps in no assemblage of the algæ have the cytological studies of recent date given such striking results as in the Rhodophyceæ. Our understanding of the life history of these forms has been quite revolutionized by the research of three investigators, Wolfe, Yamanouchi and Lewis.

Wolfe[13] from studies on *Nemalion* determined for this type that the sexual organs are not simple uninucleate cells, since the trichogyne possesses a nucleus in addition to that in the carpogonium and the sperm is binucleate and the homologue of the antheridium. The cells of the cystocarp following the fertilization of the carpogonium have nuclei with approximately sixteen chromosomes which is double the number present in the vegetative cells of the parent plant. The cystocarp must then be regarded as sporophytic in character. Because the mitotic figures in advanced stages of the cystocarps showed certain peculiarities Wolfe concluded that a reduction of the chromosomes occurred preliminary to the development of the carpospores. However, he did not trace a process of chromosome reduction through the characteristic phase of synapsis followed by a heterotypic mitosis, and on this point of his investigation more evidence is to be desired. There are certain reasons why in life histories among the Rhodophyceæ of the type of *Nemalion* the process of chromosome reduction may be expected to occur at the time of the germination of the carpospore.

---

[13] Wolfe, J. J., 1904, "Cytological Studies on *Nemalion*," *Ann. of Bot.*, Vol. XVIII, p. 608, 1904.

The investigations of Yamanouchi[14] on *Polysiphonia* established the important fact that the carpospore of this form retained the diploid number of chromosomes (forty) present throughout the sporophytic tissue of the cystocarp, and gave rise to a sporeling bearing this number in its nuclei. Furthermore, the tetrasporic plants were found to be diploid in character and the presence of the period of chromosome reduction was established in the tetraspore mother-cell. The nucleus of the tetraspore mother-cell passes through a clearly defined stage of synapsis, following which the forty sporophytic chromosomes are found associated in twenty pairs (bivalent chromosomes). The first mitosis distributes the members of these pairs and is therefore a reduction division. The tetraspore has then the haploid number of chromosomes (twenty) and on germination develops a sporeling with this reduced number, which was found to be characteristic of the sexual plants. It is reasonable to conclude that in the life history of *Polysiphonia* the sexual plants alternate with the tetrasporic, each phase arising from the spores produced upon the other. Yamanouchi expressed the belief that "the sexual plants and tetrasporic plants present two distinct phases of an antithetic alternation of generations, with the cystocarp a part of the sporophytic phase".

The many interesting points in the history of the development of the sexual organs and the cystocarps are too detailed to be presented in this brief review. Yamanouchi, however, supports Wolfe's conclusion that the trichogyne in early stages of development contains a nucleus, and that the sperm is the homologue of an antheridium, although in *Polysiphonia* this cell is uninuculeate. Some criticisms of Kurssanow[15] on the work of Wolfe upon these latter points must also be omitted.

---

[14] Yamanouchi, S., 1906, "The Life History of *Polysiphonia*," *Bot. Gaz.*, XLII, p. 401, 1906.

[15] ***Flora***, Vol. XCIX, p. 111, 1909.

A detailed study by Lewis[16] of the life history of *Griffithsia* is in agreement with the results of Yamanouchi on the essential facts of an alternation of sexual and tetrasporic plants and the behavior of the chromosomes throughout the various phases of the similar life histories. The sexual plants have seven chromosomes, the haploid number. The cystocarp presents nuclei with fourteen chromosomes and is clearly a sporophytic phase which, as in *Polysiphonia*, develops with the cooperation of the cytoplasm in certain cells of the gametophyte; the carpospores have fourteen chromosomes. The tetrasporic plants are characterized by fourteen chromosomes, the diploid number, and may be assumed to arise from the carpospores. The first mitosis in the tetraspore mother-cell is a reduction division preceded by the characteristic stage of synapsis from which the chromosomes emerge in seven pairs. Seven chromosomes, therefore, pass to the tetraspores from which the sexual plants may be expected to develop.

It is known that in a number of species of red algæ structures resembling tetraspores are occasionally found on sexual plants and that procarps are sometimes present on tetrasporic individuals. Such conditions, first observed by Bornet, have more recently been noted by Lotsy for *Chylocladia kaliformis*, Yamanouchi for *Polysiphonia violacea*, Lewis for *Griffithsia Bornetiana*, and by the writer for *Spermothamnion Turneri*, *Callithamnion Baileyi* and *Ceramium pedicillatum*. Furthermore, certain of the red algæ, as *Rhodymenia palmata* on the New England coast, present tetrasporic plants in great abundance, while cystocarpic individuals are rare or unknown. Certain critics see in the above phenomena serious difficulties for the theory of alternation of generations in the Rhodophyceæ so strongly supported by the work of Yamanouchi and Lewis.

These authors had only limited material of what seemed to be tetraspore mother-cells on sexual plants, but in this material the apparent tetrasporangia failed to mature tetraspores, the cleavage furrows proceeding only a short distance into the mother cells while the nuclei either remained undivided (*Polysiphonia*) or produced groups of several nuclei (*Griffithsia*). Thus such cytological evidence as we have on these irregularities indicates them to be abnormal developments. Examples of apogamy and apospory are now recognized as by no means uncommon in the higher groups of plants exhibiting alternation of generations, and it will not be at all surprising if such phenomena or related irregularities of life history are found among the Rhodophyceæ. Such peculiarities must of course be thoroughly studied to determine whether or not they will prove to be the exceptions that support the rule. The investigations of recent years on apogamy and apospory in the pteridophytes have in no way weakened the acknowledged alternation of generations in that group.

---

[16] Lewis, I. F., 1909, "The Life History of *Griffithsia Bornetiana*," *Ann. of Bot.*, Vol. XXIII, p. 639, 1909.

A very interesting problem is presented in the phenomenon described by Osterhout[17] of the germination of the tetraspores of *Agardhiella tenera* (*Rhabdonia tenera*) while still imbedded in the tissue of the parent plant. A peculiarity of this development is the behavior of the group of tetraspores as a unit, so that all four cells enter into the formation of a sporeling. It is important to note that the sporelings are very commonly sexual plants, as would be expected from the germination of normal tetraspores. It seems quite possible that the occasional tetrasporic shoots reported by this author are products of a tetraspore mother-cell in which the reduction mitoses have been suppressed, and therefore the tetrasporangium, behaving like a monospore, would naturally give rise to a tetrasporic plant. This is a problem which should be investigated, because if the above suggestion prove true, this behavior of the tetraspores of *Agardhiella* would present strong evidence in support of the theory of alternation of generations in the Rhodophyceæ. The peculiarity of *Rhodymenia palmata* on the New England coast, referred to above, may likewise rest upon a suppression of reduction phenomena in the tetrasporangium which would lead to the omission of the sexual phase from the life history and permit of an indefinite succession of tetrasporic plants.

---

[17] Osterhout, W. J. V., 1896, "Life History of *Rhabdonia tenera* J. Ag.," *Ann. of Bot.*, Vol. X, p. 403, 1896.

It is very important that the life histories of some of the simpler red algæ be investigated, especially such forms as have *Chantransia*-like stages characterized by the production of monospores. The fact that the reduction divisions of *Polysiphonia* and *Griffithsia* are not associated with the formation of carpospores leads one to suspect that the period of chromosome reduction in such types as *Batrachospermum* and *Nemalion* may occur at the time of the germination of the carpospore. Should this prove to be the case, the origin of the tetrasporic phase, characteristic of the higher Rhodophyceæ, may without difficulty be conceived as the result of a postponement of the reduction divisions and their association with a type of cell similar to and perhaps identical with a monosporangium. Such a postponement or delay in the expression of the reduction divisions would establish at once a plant with the diploid number of chromosomes (tetrasporic plant) and introduce into the life cycle the tetrasporangium as a new type of reproductive organ.

Lewis regards the tetrasporic plant as illustrative of "an homologous alternation of generations, not the equivalent, wholly or in part, of the sporophyte of the archegoniates", and he thereby limits the sporophytic phase in the life history to the sporogenous cells of the cystocarp. This conclusion is based on the morphological resemblance of the tetrasporic plants to the sexual, although Lewis himself points out important differences between the two. Thus "tetrasporic plants (of *Griffithsia Bornetiana*) are always more abundant, as well as on the average larger than sexual plants" a condition which is true of a number of species of the Rhodophyceæ with which the writer has had a rather extensive field acquaintance. This is a point of some importance, since too great emphasis may be placed on the resemblance in form between the two generations (a resemblance which seems most natural since the plants develop under closely similar life conditions), and important differences in size, dimensions of the cells, and general vegetative vigor may not receive the attention that they deserve. If the fusion of gamete nuclei is to be regarded as the stimulus to a sporophytic generation, the period of chromosome reduction is equally characteristic of its end, and the second event follows as a natural consequence upon the first. Mitoses with the diploid number of chromosomes whenever they occur between these two events furnish, in the opinion of the writer, the only safe criteria of the extent and duration of a sporophytic generation in normal life histories.

Yet it has become clear from recent research on apogamy and apospory that the mere number of chromosomes, whether haploid or diploid, does not determine the morphology of the generation, gametophyte or sporophyte, with which they are associated. The reasonableness of this principle is apparent when regarded from another point of view. The inheritance which is responsible for the development in a type of a sporophyte generation must be carried by the sexual phase, and the potentialities of a sexual generation must be present in the sporophyte, although in normal life histories the inheritance is latent at certain stages and only becomes operative in both generations after definite periods of development have been passed. The two germ cells, eggs and spores, do not give rise to different generations because they expressly contain a single or a double set of the chromosomes characteristic of the species; the causes of their respective developments are too complicated to be expressed in such simple terms.

To the writer the differences between the egg and the spore appear to be such as may depend primarily on a greater vigor and vitality given to the egg by the fusion of the gametes, a vigor which has expressed itself in such varied morphological manifestations because of the different conditions under which the sporophyte generations have become established in the numerous phyla characterized by their presence. The conditions affecting the sporophyte are not alone those of physical environment; there are also those evolutionary factors that operate to adjust the plant, as far as is possible, to its place among other organisms. One conclusion stands out clearly among the difficulties of these problems: as in the case of sex, the sporophyte has probably arisen independently a number of times in the evolution of plants.

So we are brought to the end of our discussion of the nuclear phenomena of sexual reproduction in the algæ to the problems of the origin of the sporophyte and the relations of the sexual and asexual generations to one another, whether or not they are essentially homologous or antithetic in the alternation of generations. It is not the purpose of this symposium to consider these matters, but allusions and inferences could not be kept out where the vital connections between the subjects under consideration and these larger speculations are so close. The immediate need of such discussion is perhaps not so great for the reason that the pages of the *New Phytologist* for 1909 have presented two important papers of Lang and Blackman representing the opposite schools together with a report of a discussion in which a number of the leading British botanists took part. That the writer's sympathies are strongly with the hypothesis of antithetic alternation of generations must have been apparent from the tenor of this paper.

CAMBRIDGE, MASSACHUSETTS,
December, 1909.

NUCLEAR PHENOMENA OF SEXUAL REPRODUCTION IN FUNGI[1]

PROFESSOR R. A. HARPER
UNIVERSITY OF WISCONSIN

In the light of recent researches the old dogma that the parasitic mode of life tends to the disappearance of sexuality has practically disappeared at least so far as the fungi are concerned. The evidence is now generally accepted that either a typical conjugation of normally differentiated gametes and their nuclei or some form of substitute for it is everywhere present.

Ernst and Schmidt on the basis of their studies on the root parasite *Rafflesia* have also recently emphasized the fact that there is no evidence in the case of seed plants that the parasitic habit tends to the disappearance of sexuality. Farmer and Digby have described a most remarkable substitute fusion in an apogamous fern and a still more striking case of substitute cell and nuclear fusions in another apogamous fern has been recently discovered in my own laboratory. It is proper under these conditions to examine anew and most critically all cases of cell fusions with reference to their accompanying nuclear phenomena and possible significance in the life cycle in question.

The study of sexuality in the fungi has also brought to light some fundamental modifications of the process of sexual fusion as found elsewhere which enlarge our conception of the nature and significance of gametic unions. It has also revealed most curious and striking substitutions for sexual fusions. I shall review briefly the most characteristic and significant of these variations from the ordinary methods of sexual reproduction. The fusion of the amœboid swarmspores to form the plasmodium of the slime moulds has never been satisfactorily accounted for, nor related to the processes either vegetative or sexual in other groups of fungi. With the increase of our knowledge of the possible variations which the sexual process may undergo it is becoming more possible to accept the conception that in some way the formation of the plasmodium may represent either an incipient or an aberrant type of gametic union in which the normal fusion of two gametes is replaced by a massing of indefinitely numerous cells.

---

[1] A paper read by invitation before the Botanical Society of America, Boston, December 30, 1909.

The cytological study of the group is only just beginning and doubtless much is to be corrected in the fragmentary observations already published. Olive, Jahn and Kraenzlein, however, agree that there are evidences of nuclear fusions either just before spore formation or earlier in the formation of the fruit bodies, and that these karyogamies are followed by synapsis and reduction divisions. The figures given show that these forms have typically developed nuclei which are favorable for fixing and staining, and indicate that whatever disagreement exists as to what occurs in the few types studied may be expected to be cleared up by further work.

The older authors were loath to regard the union of the amœbæ to form a plasmodium as involving anything of a sexual nature, but it is quite possible that we may have to extend our conception of sexual fusions at least in their primitive forms to include cases of multiple cell fusions followed by vegetative growth, and finally the fusion of the nuclei in pairs. That cell and nuclear fusions may be thus widely separated is plain from the conditions in the rusts, and in the slime moulds, as in the rusts, nuclear fusion is followed shortly by the reduction divisions.

We can not yet regard the nuclear phenomena in the slime moulds as sufficiently cleared up. In the light of what has been found in other fungi there is however certainly no ground for believing that the nuclear history in the plasmodium is as simple as the older students believed.

As directly suggestive of what may be expected in the slime moulds, we have the well-established fact of the fusing of multinucleated gametes and the subsequent pairing of all or approximately all their nuclei. Leger and others have seen that the gametes of *Sporodinia* and other zygomycetes are multinucleated, but the accounts of the subsequent processes in the zygospore can not be accepted as well founded and no one yet has been able to trace the history of these minute nuclear granules.

Stevens, however, has established the entrance of many male nuclei and their subsequent pairing with the numerous nuclei of the eggs of *Cystopus bliti* and *portulacæ* and unpublished observations made in my own laboratory have confirmed his results for *C. bliti.* I have also found such multiple fusions of about 200 nuclear pairs in the large oogonia of *Pyronema.* Claussen in a preliminary paper, while confirming the existence of the fusion of multinucleated gametes and subsequent pairing of the sexual nuclei in *Pyronema,* claims that the fusion of the pairs is not completed till they reach the ascus.

The large size of the nuclei in the ascogenous hyphæ in Claussen's preliminary figures seems to me, however, to confirm my own conclusion that the fusion is already completed at this stage. These multinucleated gametes prove convincingly that our conception of the egg and male cell must be extended to include multinucleated as well as uninucleated types. The cell at the moment of sexual union may be multinucleated as well as in its ordinary vegetative stages in the hyphæ, etc. That the nuclei fuse in pairs and not in larger numbers is further convincing evidence that they are the real bearers of the idioplasm and that the constancy of the chromosome number must be maintained by the ordinary type of doubling and subsequent reduction.

With the demonstration of the existence of coenocytic gametes the nature of the coenocyte itself becomes still clearer, as I have elsewhere pointed out. The continuous plasma membrane enclosing a coenocyte is plainly in its relation to the other cell contents to be compared with the same structure in an uninucleated cell rather than with the aggregate of membranes which bound off a mass of tissue from its environment and the cells of the tissue from each other.

It is further most interesting to note that De Bary's conception of the male element in the oomycetes as gonoplasm, a mere unbounded portion of the contents of the antheridium, has been entirely confirmed by subsequent cytological research, and it is further proof of the superior significance of the nucleus as the carrier of the idioplasm in sexual fusions that in such forms as *Cystopus candidus*, for example, it is merely one of the several nuclei in the antheridium, and that with no definitely limited cytoplasmic unit which migrates through the conjugation tube and fertilizes the egg. The differentiation of the male gamete is not here an ordinary process of cell division, but a mere flowing out of one of the nuclei of the coenocytic antheridium.

The most striking discovery as to fusion in the fungi and the one which preceded and led the way to very many of the more important later results was the observation by Wager of paired nuclei and the subsequent fusion of these nuclei in the young basidium.

Wager was mistaken in describing a series of such fusions by pairs, but the clear account of the nuclear structures which he gave and the evidence that nuclear division occurs by a karyokinesis like that of other plants and animals showed for the first time the possibility of determining the nature of the various reproductive bodies in fungi by a more exact cytological investigation of them than had before been thought possible.

Wager brought the first proof of the existence of an endokaryogamy—the fusion of nuclei not derived from separate and independent gametes as in ordinary fertilizations, but having had a similar if not identical history in the cells from which the basidium arose. Such a process was entirely unknown before in either plants or animals.

Subsequent investigations by Dangeard, Maire, Ruhland, Nichols, myself and others have shown that in the Basidiomycetes a long series of binucleated cells precedes the formation of the basidium and the nuclear fusion in it may well have something of the value of a union of differentiated gametic nuclei.

The origin of the binucleated cells in the Basidiomycetes does not apparently result from a cell fusion at a definite point in the life cycle, as is the case in the æcidium of the rusts. Such a fusion might perhaps be expected to be effected at the origin of the carpophore, but it has been established that binucleated cells may be present in the mycelium prior to the formation of the carpophore. Series of such cells may extend back almost if not quite to the germination of the spore from which the mycelium arose.

A fusion of gametes morphologically equivalent to those of other algæ and fungi seems to have quite disappeared from the group so far as known at present, though it is to be remembered that comparatively few forms have been investigated as to the early stages of the formation of the carpophore. It seems probable that the endokarygamy in the basidium may have functionally replaced an older fusion of differentiated sex cells.

We have then on the present evidence a large group (over 9,000 species, according to Saccardo) of saprophytic and parasitic organisms in which normal sexual reproduction has been replaced by the fusion of nuclei of probably separate descent through a long series of cells, but which are contained at each stage within the limits of a single cell body.

The most thoroughly worked out modification of sexual reproduction in the fungi is the fusion of uninucleated gametes producing binucleated series of cells in which nuclear fusion follows only at a much later period. Such fusions seem probably to be present in all rusts which have an æcidium or primary uredo and may occur in two forms involving in the one case merely the migration of a nucleus into a so-called fertile cell which then develops into the chain of æcidiospores, while in the other case there may be a complete cytoplasmic union of equivalent cells the so formed binucleated fusion cell then developing into a row of æcidiospores or a series of primary uredospores.

Dangeard and Sappin Trouffy discovered that the binucleated cells in the rusts originate with the æcidium, but the real significance of the binucleated condition and the method of its origin first became clear with the work of Blackman, Christman and Olive.

It is quite probable, as Blackman maintains. that these fusing cells in the æcidium of the rusts have been much modified from the ancestral conditions of the sex cells of the group, so that their fusion is to be properly characterized as a vegetative fertilization. Still there can be no question that functionally these are sexual unions, and we can hardly imagine anything more illuminating as to the relations of the male and female pronuclei in the cells produced by fusion and hence containing the double chromosome number. There can be no question here that the male and female chromosomes maintain their independence throughout the entire sporophytic life cycle and that nuclear fusion and synapsis are two closely associated phases of that more intimate union of the chromosomes which the behavior of hybrids suggests must occur at the close of the sporophyte. Such a series of binucleated cells is unknown among animals but the tendency to persistent independence shown by the pronuclei in the embryonic development of *Cyclops* shows that there is every reason for believing that here and probably in all nuclei with $2n$ chromosomes the hereditary idioplasms from the male and female parents maintain quite the same physical independence throughout the sporophyte as is so convincingly shown in the rusts.

The phenomena of conjugate division also indicate very clearly how the mechanism of karyokinesis, including centrosomes, asters and spindles, may be partly or wholly combined in a single system without necessitating a similar union of the idioplasmic units.

One of the most important points in this sexual process in the rusts is that the nuclei do finally fuse in the teleutospore. One might suppose that since the nuclei can function as physically independent units through the whole life of the sporophyte with its manifold vegetative and reproductive phases, a reduction division might be accomplished by the mere insertion of a wall between the conjugate nuclei. This may be what occurs in *Endophyllum* according to Maire. Still the fact that the nuclei fuse before the heterotypic division in practically all other rusts is certainly strongly suggestive that synapsis and its accompanying phases represent a stage of mutual influence if not of interchange of physical material between the chromosomes much more intimate than any which has preceded it in the life of the sporophyte.

On the other hand, it is plain that the nuclear fusion is unnecessary so far as the sporophyte itself is concerned. The sporophyte of the rusts, as in other plants, is the distinctively dominant and progressive phase in the life cycle of the fungus. The uredo mycelium and the rapid succession of crops of uredospores with all their adaptations for rapid spread and virulent development are a parallel in every respect to the sporophyte in every type of plant in which it is found from the ferns to the seed plants. It is plain then that the vigor and adaptability of the sporophyte are not dependent upon the combination of the sets of parental chromosomes in a single nucleus. The same results are possible with two more or less independent nuclei in the cell, each containing the chromosomes from one parent.

For the ascomycetes Dangeard extended Wager's observation of endokaryogamy in the basidium by the discovery of a nuclear fusion in the ascus similar to that in the basidium and teleutospore. Dangeard pronounced these nuclei which fuse in the ascus the morphological equivalents of the gametes of other fungi and algæ and the resulting ascus a fertilized egg; a view in which he has not been followed by other students of the group. It seems probable, however, that this fusion functionally may have the value in greater or less degree of a sexual fusion, and that in cases in which the normal union of gametes has disappeared this endokaryogamy may be a substitute for it.

The most puzzling feature of the sexual reproduction in the ascomycetes and that about whose existence, I may add, there is least agreement, lies in the fact that in the course of a single life cycle we have two nuclear fusions. At the origin of the ascocarp we find the formation and fusion of normally developed sexual cells and nuclei and in the young ascus a fusion of included nuclei. There is practically no dispute at present that the gametes formed at the origin of the ascocarp represent the original and normal sex organs of the fungus and for *Pyronema* the fusion between the antheridium and trichogyne is universally admitted.

My own studies have convinced me that in the mildews and *Pyronema* at least we have a normal conjugation of differentiated gametes at the origin of the ascocarp and an endokaryogamy in the ascus.

Blackman and Fraser confirm the existence of the two fusions in *Sphærotheca* and Blackman and Fraser (1906, *Humaria granulata*), Fraser and Chambers (1907, *Aspergillus Herbariorum*), Welsford (1907, *Ascobolus*), Fraser (1908, *Humaria rutilans*), Cutting (1909, *Ascophanus*) and Dale (1909, *Aspergillus repens*) describe the occurrence of two endokaryogamies in a single life cycle.

As already noted, Claussen in a recent preliminary paper attempts to resolve this difficulty in *Pyronema* by claiming that while there is a normal cell fusion at the origin of the ascocarp the nuclei of the gametes do not fuse, but are paired and divide by conjugate division in the ascogenous hyphæ, fusing only after they reach the young ascus. This is a direct transference to the ascomycetes of the conditions described by Blackman and Christman for the rusts, and it is certainly an obvious and easy suggestion. It was made in a letter to the writer by Raciborski in 1895 and later published by him.[1] In my opinion, as noted above, judging from the size of the nuclei in Claussen's figures of the young ascogenous hyphæ, the nuclear fusion has already occurred at this stage.

It is evident that such profound changes as have led to the wide-spread occurrence of endokaryogamy among so many and such diverse groups of the fungi can hardly have come about suddenly. Even on the mutation theory it would hardly be supposed that in the rusts, for example, the disappearance of function in the spermatia, the new fusion in the æcidium, the long series of conjugate divisions in the destructive uredo stage of the fungus and the endokaryogamy in the teleutospore should all have appeared by a single step simultaneously. There is a degree of correlation in all these changes without doubt, but they must fairly be assumed to have worked themselves out gradually in connection with the development of the complicated life history with heterœcism and the numerous spore forms which characterize the group.

It is evident that at present the fusion of nuclei in the teleutospore is simply the delayed union of the gametic nuclei that came together in the cell fusion at the base of the row of æcidiospores. In my opinion, however, as I have argued at length elsewhere, this fusion in the spore mother-cell originated as a purely vegetative union associated in the ascus and basidium with the development of the relatively gigantic size of these cells and the maintenance of the nucleo-cytoplasmic relation, the factors involved being the abundance of nutritive material concentrated in the ascus and basidium as sporebearing or-

---

[2] *Flora,* 1896, p. 132.

gans and their function as spore mother-cells which are to undergo reduction divisions and close the sporophyte generation.

From this standpoint it is to be remembered that we have considerable evidence that in the rusts with abbreviated life cycles the binucleated condition and conjugate division extend back from the endokaryogamy to more or less vague and uncertain points in the life cycle of the sporophyte. For example, in the short-cycled rusts with only teleutospores Blackman, Maire and Olive find that the binucleated condition extends back from the teleutospore to some undetermined point in the mycelium from which the teleutospore sorus arises. As already noted, it is certain that in various basidiomycetes the binucleated condition extends back through the carpophore to some not sharply marked stage in the mycelium. Similar conditions may be present in the smuts.

In *Pyronema* I have found that the paired nuclei in the young ascus arise by simultaneous division of two mother nuclei in the tip of the ascogenous hypha from which an ascus is to arise and that the spindles are so placed that the two nuclei which are cut off in the young ascus and subsequently fuse are not sister nuclei. This final nuclear division is similar to the conjugate nuclear divisions in the rusts. Recently Guilliermond and Maire have described cases among certain of the larger discomycetes in which the ascogenous hyphæ were found to consist of binucleated cells for some distance below the young ascus, and suggest that these are comparable to the binucleated series of cells in the rusts. In the majority of cases so far described the ascogenous hyphæ are multinucleated as in *Pyronema* and *Ascobolus*. In the mildews the cells of the ascogon below the ascus are uninucleated and it does not appear that the nuclei which fuse in the ascus come from any such distinct lines of nuclear descent as do those which fuse in the teleutospore of the rusts.

The binucleated condition may be working backward from the endokaryogamy in the ascus in the forms noted by Guilliermond and Maire, and further we have no cases as yet in which the binucleated condition originating in a cell conjugation without nuclear fusion is working forward into the sporophyte. In the full-cycled rusts the binucleated condition and conjugate division extend from the gametic union to the reduction stage in the spore mother-cell. This is manifestly a condition of equilibrium comparable to the stable conditions present in most forms with definitely limited alternation of generations. In *Pyronema* in case Claussen's preliminary contentions should turn out to be true the same condition would be presented. We have nowhere evidence that the binucleated condition and conjugate division originated in gametic fusions and worked gradually forward through the sporophyte.

As perhaps the most striking evidence that the saprophytic habit has not led to the disappearance of sexuality we have the recent evidence as to the occurrence of sexual fusions in the yeasts. It is probably too early to speak with definiteness as to nuclear phenomena in these minute cells. Still there can be no question that in *Zygosaccharomyces* we have normal conjugation of gametes followed by two divisions and spore formation quite probably representing a reduction stage. In *Saccharomyces Ludwigii* just as clearly a double division period and endospore formation is followed by conjugation. This transposition of the sexual stage may be secondarily developed as Guilliermond believes, or may indicate the polyphyletic nature of the yeast group. There can at least be no question that sexuality either in a primitive or modified form has been maintained in this otherwise highly specialized saprophytic group.

Our knowledge of the conditions in the smuts as the result of the work of Dangeard, myself, Federley and Lutman, in a paper now in press, indicates that in this group also two fusions may occur in a single life cycle but under conditions which make the relations of the two to each other and to the original sexual reproduction of the group much clearer. In the smuts we have an endokaryogamy in the smut spore. In *Entyloma* the mycelium from which the spore arises is binucleated at least in the later stages of its development. In *Ustilago* the mycelial cells are multinucleated and there is less evidence for the separate ancestry of the nuclei in the smut spore.

The conjugations of the conidia regarded by DeBary as sexual unions represent the only normal conjugation of gametes in the life cycle, but they are plainly only of sporadic occurrence. Certainly they are not necessary to the completion of the normal development of the smut and they may probably be assumed to be in process of disappearance. The behavior of the nuclei in these fusing conidia favors this view. Federley finds them fusing in normal fashion in the smut of salsify. Lutman finds also that the nuclei may fuse in the conjugation of the promycelial cells of the oat smut. Dangeard finds they do not fuse in the conidia of *Tilletia* and according to my own observation the same is true in the conjugation of the conidia of the anther smut, though here many of the ordinary effects of sexual fusion appear in the conjugated pairs of conidia.

Lutman shows that infection and the normal development of oat smut may occur without any such fusions, and that hence the later nuclear fusion in the smut spore can not possibly be a delayed fusion of nuclei which came together in an earlier normal cell fusion of gametes. The endokaryogamy in the smut spore appears here as a distinct process which has originated independently of the normal sexual fusion, though it may have secondarily developed sexual significance with the development of conjugate division in the mycelial cells from which the smut spores arise, and have thus made possible the entire disappearance of the original normal sexual reproduction.

From this standpoint we are justified still further in the assumption that the appearance of binucleated cells and possibly conjugate division in the ascogenous cells of the discomycetes mentioned above indicate not the persistence of unfused but paired gametic nuclei, but a working back of conjugate division from the spore mother cell into the tissues of the sporophyte, thus giving gradually to the endokaryogamy in the ascus more and more of a sexual significance.

The evidence has accumulated in many lines that in several groups of the fungi the sexual process is followed by a longer or shorter period of development with cells containing a double chromosome number. Evidence from a direct counting of the chromosomes before and after fusion is lacking, owing to the small size of the nuclei, still there can be no reasonable doubt that the regularly binucleated cells of the rusts which form an unbroken series from the æcidium to the teleutospore contain twice the number of chromosomes present in the uninucleated mycelial cells from which the æcidium arises. As already noted, the conditions in the rusts are especially favorable for demonstrating that the sexual fusion inaugurates a period of development with cells containing 2n chromosomes and that this sporophytic stage tends to predominate in the life cycle both as to length and complexity.

It is quite evident also in advance of a knowledge of the complete cytological data that the double division involved in forming the promycelial cells is to be considered as a reduction period.

In the smuts and Basidiomycetes the limits of the gametophyte and sporophyte are not so definitely marked as in the rusts, but the binucleated phase is certainly to be regarded as sporophytic however it may be inaugurated. In the Ascomycetes the morphological relations of the mycelium and ascocarp have long been regarded as showing a parallelism with the conditions in liverworts and mosses. The fact of a triple division in the ascus in contrast with the elsewhere universally present double division of spore mother cells has been regarded as opposed to the interpretation of the ascus as a spore mother cell. However, as I have pointed out, this triple division replacing ordinary double division is to be regarded as correlated with two nuclear fusions preceding it.

Miss Fraser has brought further interesting cytological evidence that the third division in the ascus is a reduction division which she characterizes as a brachymeiosis. The universality of the triple nuclear division in the ascus even in cases where less than eight spores are formed is certainly to be regarded as a fact of the first importance and comparable to the universality with which a double division occurs in other spore mother cells. The most striking of the peculiarities as to cell and nuclear fusions in the fungi may be summarized as follows:

1. The fusion of multinucleated gametes.
2. The male element may be a mass of gonoplasm rather than a definitely bounded cell.
3. Endokaryogamy, the fusion of nuclei not brought together by cell fusion but of more or less independent ancestry.
4. The fusion of gametes without the fusion of their nuclei; the latter reproducing by conjugate division for long series of cell generations and finally fusing just before the reduction division.
5. Fertilization by nuclear migration from a vegetative cell to an egg or fertile cell.
6. Two successive fusions in the same life cycle, a normal conjugation of gametes and later endokaryogamy.

THE POSE OF SAUROPODOUS DINOSAURS[1]

DR. W. D. MATTHEW

American Museum of Natural History

These four articles discuss a question of considerable general interest. Did the huge Sauropodous dinosaurs, *Diplodocus, Brontosaurus* and their allies, walk like elephants, or crawl like crocodiles? The skeletons and casts in the larger museums of America and Europe have all been mounted straight limbed, with the body well clear of the ground. But the evidence for giving them this pose, so different from that of the generality of reptiles, although well known to those who are responsible for it, has not until recently been published. Hence it is not surprising that these reconstructions have been criticized more or less seriously, especially in Germany, and that two writers of high scientific standing—Dr. Tornier in Berlin, and Dr. Hay in Washington—have contended that these animals could not have walked upright, but must have dragged the belly on the ground as crocodiles and lizards normally do. Both writers have attempted and discussed at length the re-articulation of the skeleton in the crocodilian pose.

Dr. Tornier's argument is, briefly, that reptiles crawl while mammals walk; that *Diplodocus* is a reptile and resembles the lizards and crocodiles far more closely than it does any mammals in the details of construction of the shoulder- and hip-girdles, limbs and feet. Therefore, it should be posed like one of the larger lizards, except for the long neck, which he compares to the long-necked birds and poses in accordance. A sketch restoration and a number of diagrammatic drawings illustrate his views. The subject appears, frankly, to be somewhat outside the range of his studies, and his comparisons are not broad or thorough enough to be at all convincing.

---

[1] "Die Rekonstruktion des Diplodocus," von O. Abel, *Abh. k. k. Zoöl.-Bot. Gesellschaft in Wien*, Vol. V., 1909–10, pp. 1–60 of separata, three plates and text figures; March 24, 1910.

"Review of some Recent Criticisms of the Restorations of Sauropod Dinosaurs Existing in the Museums of the United States, with Special Reference to that of *Diplodocus Carnegiei* in the Carnegie Museum," by Dr. W. J. Holland, American Naturalist, 1910, Vol. XLIV., pp. 259–283, plate I. and text figures, May, 1910.

"On the Manner of Locomotion of the Dinosaurs, Especially *Diplodocus*, with Remarks on the Origin of the Birds," by Oliver P. Hay, *Proc. Washington Acad. Sci.*, 1910, Vol. XII., pp. 1–25, pl. 1, text figs. 1–7, February 15, 1910.

"Wie war der *Diplodocus carnegii* wirklich gebaut?" von Gustav Tornier, *Sitz.-ber. Gesell. Naturf. Freunde zu Berlin*, 1909, pp. 193–209, pl. II. and 6 text figures.

His criticisms are very effectively and completely answered by Dr. Abel and Dr. Holland. These authors point out that while the dinosaurs were reptiles and as such their bones were constructed upon the reptilian plan, yet they form a group apart, differing from other reptiles and in many respects resembling the struthious birds; that these resemblances, especially as regards the construction of pelvis and hind limbs, leave no reasonable doubt that the typical dinosaurs walked pretty much as do the great ground birds; that the limbs of *Diplodocus* and its allies differ from the normal dinosaur type in a marked superficial and adaptive resemblance to the elephant, indicating a quadrupedal "rectigrade" mode of motion; that the skeleton articulates satisfactorily in this pose and that the attempt to articulate it in the pose of a crocodile or lizard involves either a demonstrably false interpretation of parts, or a disarticulation of the joints which proves such a position to be highly abnormal if not utterly impossible for the creature to assume.

Dr. Hay's contributions to the discussion—the article cited and an earlier one in the AMERICAN NATURALIST—are worthy of more careful consideration. Hay is a high authority on fossil vertebrata, especially upon Chelonia and fishes, and has recently devoted considerable study to the dinosaurs. He recognizes the fact that the dinosaurs, while pertaining to the class Reptilia, form a group apart, with many analogies to the birds; that many dinosaurs did walk with the body clear of the ground, and that many lizards walk or run in this way at times. He does not deny that even the Sauropoda may have done so at times, but regards them as too massive and heavy for this to have been their normal mode of progress. But his chief protest is against the placing of the knee and elbow joints in sagittal planes (*i. e.,* bending parallel with the middle line of the body) as in mammals, instead of bending outward as in all modern reptiles. In certain points of his argument he makes out a convincing case in the reviewer's opinion; other points may be satisfactorily answered.

Dr. Hay misstates the supposed significance of the peculiar type of femur seen in *Diplodocus.* He observes:

> If the mammal-like gait of *Diplodocus* be insisted upon on the ground of straightness of the femur, it may be pointed out . . . that the femora of *Sphenodon* and of lizards, animals that creep, are straight. If it be contended that it is in the heavy-bodied animals that a straight femur is correlated with a lifting of the body from the ground during locomotion, it may be permitted to recall that the femora of *Allosaurus* and *Tyrannosaurus,* great carnivorous dinosaurs, are distinctly bent. The femora of *Trachodon* are straight, while those of *Camptosaurus* and *Laosaurus* are curved. Curvature of the femur seems therefore to have no relation to size of body or erectness of pose.

But no one, so far as the reviewer knows, has asserted that the straightness of the shaft of the femur of *Diplodocus,* considered alone, proved that the animal walked like a mammal. For among mammals there are both straight and curved femora, and a wide variety of gaits.

The argument that Dr. Hay presumably has in mind is this: That in the elephants and several other types of gigantic mammals the femur is relatively long, straight-shafted, with its articulations terminal rather than lateral, the feet short, rounded, heavily padded and capable of but limited motion, the whole limb being pillar-like and normally held straight under the body. All gigantic mammals show some degree of approach towards this type of limb; and in the Sauropoda the resemblance in form and proportions is very marked. The same type is seen in *Coryphodon, Uintatherium, Titanotherium, Arsinoitherium, Pyrotherium, Astrapotherium, Dipro-*

todon, gigantic mammals of widely diverse stocks, in *Stegosaurus* and *Triceratops* among the dinosaurs, and an approach towards it in various other groups. The modern horses, rhinoceroses, cattle and other large animals, and most of the very large extinct mammals show a distinct approach toward these proportions as compared with their smaller and more agile ancestors; so too do the gigantic *Trachodon* and *Tyrannosaurus* as compared with their smaller and more agile ancestors or relatives, *Laosaurus, Camptosaurus,* and *Allosaurus.*

On the other hand, a glance at a lizard femur shows that the straight shaft is associated here with a wholly different position of the proximal and distal articulations and of the trochanters by which the limb is moved. The distal articulations for the tibia and fibula are on the back of the femur, not on its end; the great trochanter for the hip muscles projects outwards from the shaft instead of upwards in line with it; the feet are long and the toes relatively elongate; there is very little padding.

The shaft of the femur is nearly straight in the aquatic turtles and the articulation for the lower limb is quite distal in position; but the trochanter projects upward, the limb is carried outward from the body and more or less straight. In the land turtles and in the crocodiles the femur has a strongly curved shaft, bent downward at the distal end, the limb still projecting outward from the body but flexed sharply downward at the knee. Here then are two distinct methods by which a swimming limb may be converted into a crawling limb.

The straight-shafted femur does not *per se* prove that *Diplodocus* walked in any of the various ways that mammals walk. But taken in connection with the numerous other adaptive resemblances in form and proportions of the bones of the hind limb, feet and pelvis, to the elephants and other gigantic mammals and reptiles cited, it does afford a very strong argument for asserting that *Diplodocus* walked like an elephant as to its hind limbs.

Dr. Hay's next point appears to be a strong one. He observes that if we compare the femora of such dinosaurs as *Allosaurus, Tyrannosaurus, Trachodon* or *Camptosaurus,* admittedly erect-walking bipedal forms, with the femora of the Sauropoda, we find a great difference in the quality of the bone and the finish of the articulations.

> The shaft of the former appears to be more elaborately modelled, and to consist of finer and harder bone; all the articular surfaces are smooth and they carry the conviction that the original surfaces, barring a thin layer of cartilage, are preserved; there is a definite head, separated from the shaft by a distinct neck, and nearly filling the acetabulum; and there is a definitely formed trochanter major. In the Sauropoda, on the contrary, the shaft seems to be composed of coarser bone; the articular surfaces are rough and show that they were covered by a thick layer of cartilage; the head merges imperceptibly into the supposed great trochanter and into the shaft; [it would be more accurate to state that the great trochanter is not a separate process but a rugose area marginal to the head of the femur] and the head lacks much of filling the acetabulum. In its [*sic*] low stage of differentiation the femora of the sauropods resemble greatly those of the crocodiles and are hardly above those of the lizards.

It is not clear what lizards Dr. Hay had here in mind. The larger land lizards have a much more "differentiated" femur. Even in the crocodiles the resemblance is not very close. But a much closer and more striking resemblance in the characters cited may be found if we compare the femora of large *aquatic* reptiles, ichthyosaurs, mosasaurs or plesiosaurs, or large *aquatic* mammals such as the Cetacea, with the femora of the Sauropoda. The reviewer would agree entirely with Dr. Hay that the lack of differentiation and finish in the limb bones of Sauropoda is a strong argument that they were not adapted to the habitual support of the whole weight of the body. But the evidence cited accords exactly with the theory of Owen and Cope that they were wading animals, and the limbs were designed for the support of the body in the water, with most of its weight buoyed up thereby.

Dr. Hay believes that the position of the great trochanter in the Sauropoda was well down on the shaft, as it is in the Triassic Theropoda; but he fails to give any good reason for rejecting Osborn's view that the very clearly marked rugosity around the proximal-external angle of the head is the area of attachment of the gluteal muscles.

The character of this rugosity is certainly that of an attachment for powerful muscles; its position is substantially that of the distinct process in the larger bipedal dinosaurs; while the surface where Dr. Hay would locate the attachment is a surface of smooth bone. On the other hand, the view of Marsh and Hatcher, apparently shared by Holland, that the entire proximal-external angle, including part of the rugose surface of the proximal end, similar in character to the rest of the anatomical head or articulating surface, is the great trochanter, appears to be indefensible, and Dr. Hay's arguments conclusive as against it. This view seems to have been founded on the analogy with the proboscidean femur, carried further than the facts warrant. But Dr. Hay's conclusion that the femur of the Sauropoda represents a very early stage in progressive adaptation of the limb from the primitive swimming to the walking type, is not warranted if Osborn's view as to the position of the trochanter be correct, for as Hay rightly observes, in the progressive stages of adaptation to upright carriage this attachment moves up towards the head of the bone. But the only semblance of argument that Dr. Hay offers against this view seems to be the assumption that *Diplodocus* was more primitive than its Triassic predecessors. The truth seems to be that the Sauropoda were highly specialized as regards the adaptations for upright walking, but degenerate as regards the adaptations for bearing great weight on the limbs.

As to the aquatic habitat of the Sauropoda, Dr. Hay's statement of the evidence can hardly be regarded as a fair one, although he seems to be of the opinion that the larger forms, at any rate, were secondarily aquatic.

> The ability of any large animal to walk about thus submerged must depend on its having a massive skeleton, as have the hippopotamus and the manatee. In *Diplodocus*, on the contrary, almost every conceivable device has been used to reduce the weight of the skeleton. The great vertebræ contain large and small internal cavities, while externally the processes are carved into thin plates and buttresses, and the centra are deeply excavated on each side. Moreover, as has been shown by Hatcher, the limb bones are hollow. It would seem to have been hardly

more possible for *Diplodocus* to walk about immersed in water than it would be for a man to do the same.

In a brief description of the *Brontosaurus* skeleton[2] which Dr. Hay consistently ignores, although he can hardly fail to be acquainted with it, the reviewer pointed out that there was a very marked difference in the massiveness of the upper and lower parts of the skeleton in the Sauropoda. All the bones above a line passing through the acetabulum and glenoid cavity of the scapula are very lightly constructed, and thus far Dr. Hay's statement is correct. All the bones below this line are, on the other hand, very massive, and solid or nearly so. So far as the reviewer can judge from comparison of a large series of bones, they are quite as dense and massive as the corresponding bones in the hippopotamus; and they certainly are not hollow in the sense that the bones of *Allosaurus* are hollow. All of them are cancellous towards the center, and in the femur there is an open cavity of proportionately small size in the shaft. But they are certainly far more dense than in the elephant, and wholly lack the devices for lightening the weight that are so conspicuous in the skull, cervical and dorsal vertebræ, the first few caudals, the ilium and the proximal ends of the ribs. The median and distal caudals, the ischia, pubes and limbs, the shoulder-girdle, except for the blade of the scapula, and especially the feet, must be wholly excepted from Dr. Hay's statement in regard to the lightening of the skeleton; they are certainly unusually massive in form; and while the precise degree of density of the petrified bone is not very easily compared with modern bone, yet in the reviewer's opinion they compare most nearly with the bones of aquatic animals, such as plesiosaurs and mosasaurs among the reptiles, cetaceans, pinnipeds, sirenians and hippopotami among the mammals, and are materially exceeded in density only by the sirenians.

Dr. Hay's observations in regard to the pose of bipedal dinosaurs form an interesting corollary to his views in regard to the Sauropoda. For although admitting that they were in general bipedal and walked with the body clear of the ground, he finds himself compelled, in the logical development of his theories, to assign them a widely straddling walk. This compels him to explain the observed tracks of *Iguanodon,* which are not straddling, as being an unusual mode of progression associated with slow walking, but that if the animal had been running it would have had a wider trackway. So far as the reviewer's observations extend, the faster an animal is walking or running the more it is inclined to plant the feet close to the median line of its trackway, and the less likely to waddle—this is assuredly true of our own gait, and probably holds good with any bipedal animal. The stronger evidence derived from the numberless tracks of the Connecticut Valley Triassic, Dr. Hay would explain by supposing that these tracks were made, not by dinosaurs which we know existed, but by birds of whose existence at that time we have no evidence.

---

[2] Amer. Mus. Guide Leaflet No. —, 1905.

But Lull has shown that not only do many of these tracks correspond precisely and in detail with the reconstructed hind feet of carnivorous dinosaurs, but the occasional impressions of the fore feet, the pubes and the tail, correspond equally well. A disputed hypothesis in regard to the amount of straddling in their gait is hardly sufficient ground to question the accepted view that these tracks were made by dinosaurs.

It is indeed quite reasonable to suppose that ancestors of the birds, more or less closely related to the dinosaurs, were living during the Triassic. But the extreme rarity of bird remains during the whole Mesozoic, and the fact that, with the exception of *Archæopteryx,* the better known forms are highly specialized aberrant types, gives ground for supposing that the normal habitat of Mesozoic birds was such that their remains were not buried in the areas of sedimentation. They were presumably confined to the higher and drier uplands, remote from the river-deltas and coastal swamps which were the normal habitat of the heavy and bulky dinosaurs, and which the lighter and smaller dinosaurs of the upland visited to a greater or less degree.

Dr. Hay makes considerable use in his discussion of Marsh's restoration of *Anchisaurus,* as in this reconstruction the limbs appear relatively shorter and the proportions more lizard-like than in most Theropoda. But while this is true to some extent of *Anchisaurus* and apparently of most Triassic Theropoda, it is exaggerated in Marsh's reconstruction by insertion of several additional dorsal vertebræ which are probably not warranted.[3] The restoration is a composite from two or three partial skeletons; the number of vertebræ is really uncertain. If the body be shortened to the proportions of the more completely known dinosaurs, there is less difficulty in supposing the animal to have been habitually bipedal, and bird-like in gait. The general contention that the dinosaurs evolved from a crawling lizard-like gait to a bipedal bird-like gait without passing through a quadrupedal walking mammal-like gait appears probable enough. But the Sauropoda seem to be most easily explained by the hypothesis that they acquired secondarily a quadrupedal elephantine gait, that they were at first more or less amphibious and finally exclusively aquatic waders.

Whether we state, as does von Huene, that the Sauropoda are derived from Theropoda, or, as Dr. Hay will have it, that the Theropoda are derived from Sauropoda seems to be largely a question of terms and definitions. Both are derivable from a common ancestral group, but the Sauropoda have specialized fully as much in one direction as the Theropoda in another. In fact, in the present writer's opinion, the Sauropoda are decidedly more specialized, although their specialization is in part degenerative and a re-adaptation to the aquatic environment of the remote ancestors of the Reptilia.

---

[3] Marsh has inserted additional dorsal vertebræ in most of his dinosaur restorations, as may be seen by comparison with the more complete skeletons which have since been mounted and described in several American museums. There are three too many in *Brontosaurus* (Riggs), five too many in *Camptosaurus* and six too many in *Triceratops* (Gilmore) and so on probably throughout. His general concept of the analogy of the group seems to have been too much lizard-like and not enough bird-like.

Dr. Holland's article is a brilliant, well-illustrated and cruelly convincing polemic in support of the accepted pose of the *Diplodocus* skeleton, but in the reviewer's opinion he does not at all do justice to the real weight of some of the arguments advanced by Hay and Tornier, especially the former. Serious exception might be taken to the positiveness of some of his assumptions, as well as to the ridicule of his opponents' views.

Holland shows by aid of a series of photographs and carefully finished drawings that the pose advocated by Dr. Tornier could not have been assumed without an entire dislocation of the important limb joints; that the pelvis of the sauropods is like "the pelves of the dinosauria in general, distinctly ornithic in type, not lacertilian nor crocodilian," that the body is deep, narrow and short as in birds, while in the crawling reptiles it is broad flattened and more elongated; that the scapula and fore-limb differ in important features from those of crocodiles and lizards, and the fore limb can not be articulated in a crawling pose; that the long heavy tail affords no argument for a crawling posture; that the feet are digitigrade and not plantigrade as asserted by Tornier; that the general form and proportions of the limbs point to an elephantine pose, and that the single known footprint of a Jurassic Sauropod supports the same interpretation. (It is worthy of note that Dr. Lull has carefully examined this footprint and come to the conclusion that it was probably made under water rather than on land.) The whole article is very readable and clearly written, and would seem to close the case so far as the possibility of Tornier's reconstruction is concerned.

Dr. Abel's contribution is a careful, thorough and fair-minded consideration of the problem by a high authority upon fossil vertebrates, who has devoted a great deal of time and thought to paleontologic reconstructions. He reviews the principles governing such work, the relationships of *Diplodocus* and the data for the reconstruction, the opinions that have been held in regard to the pose and habits of the Sauropoda, and cites Tornier's arguments in some detail. He then gives a careful and critical presentation of the evidence afforded by the form and relations of the different parts of the skeleton. He concludes that the generally accepted poses, as shown in the several skeletons of Sauropoda that have been mounted, and in the published restorations by Marsh, Hatcher, Holland and Osborn, are in the main correct, except that the scapula should be somewhat more vertical, the elbow directed more outward, and fore and hind foot completely digitigrade. He finds no warrant for the radical changes in pose recommended by Tornier and Hay. The evidence can not well be condensed within the limits of a review. The marked analogy to the elephants, especially in the proportions and relations of both fore and hind feet, and in the limb bones the relationship to the bipedal dinosaurs, much closer than to the crawling reptiles, the mechanical requirements for the support of a body of the size and proportions of a Sauropod dinosaur, are the chief criteria used to interpret the direct indications from the bones of the *Diplodocus* skeleton.

Dr. Abel's conclusions may be condensed from his summary as follows:

1. The animal did not crawl, but walked, with the body well clear from the ground, the knee bending forward, the elbow outward and backward, the feet digitigrade as in the elephant. In a standing position the angle at the knee was slight (15°), while the bend at the elbow was more considerable (60°). The fore feet were longer and more completely digitigrade than the hind feet; both fore and hind feet were exaxonic, the weight of the body resting chiefly on the outer digits, which were heavily padded, with rudimentary toes, while the innermost toe of the fore foot and the inner three toes of the hind foot bore large blunt claws.

2. The body was deep and narrow, strongly arched from front to back, the neck long and flexible, normally carried forward, with the head continued in the same direction.

3. There were twelve thoracic vertebræ, of which the

first is unknown; and sixteen cervicals, of which the first (pro-atlas) is unknown. The problematic bone identified by Holland as clavicle, by Nopsca as os penis, by Tornier as episternum, is the first rib.

Some of the points cited may be questioned or disproved,[1] but the main contention, that the Sauropoda were walking, not crawling animals appears to be abundantly proved.

Nevertheless, there is a great deal yet to be said on the pose and habitat of the Sauropoda, and there are certain lines of evidence which none of the authors cited have considered adequately.

In the first place, the nature and cause of the parallelism between sauropod dinosaurs and elephants has not been very clearly pointed out. The type of limb and foot structure which they show in common was first clearly defined, so far as the reviewer is aware, by the late Professor Gaudry, under the name of "rectigradism." It is a specialization directly associated with gigantic size, the limb becoming straight and pillar-like, the foot short, round, heavily padded, with toes reduced or vestigial. The movements of the limb are chiefly at the upper joints, the foot serving chiefly as pad or cushion to absorb the shock in locomotion. This is very different from the typical "digitigradism" of the dog or cat; it may be observed with modifications, in large plantigrade and unguligrade animals as well as in digitigrade forms, and a progressive approach towards it may be observed in all races of land vertebrates as they approach gigantic size. The proximal segments of the limbs tend to become longer and straighter, their articulations more terminal, the distal segments shorter, their range of movement decreasing, the toes become much shortened and vestigial, buried in an elastic pad, or, as in ungulates, with a broad horny hoof, which absorbs shock less completely but gives a firmer footing.

---

[1] The insertion of two additional dorsal vertebræ is certainly erroneous, and with this falls to the ground the interpretation of the "clavicle" as a rib. Positive evidence from other partially articulated skeletons is likewise available, I believe, to determine the number of cervical vertebræ.

Obviously a specialization of this kind will occur only in an animal which habitually rests its weight on the limbs, and it is necessary with increased weight, because the increase of weight varies as the mass (cube of the linear dimensions) while the increase in strength varies as the cross section (square of the linear dimensions).

This last circumstance will very clearly set a limit to the size that an animal may attain as a practical working mechanism. And here we are brought to face an unanswerable difficulty if we consider the Sauropoda as land animals. How is it that with their less perfect reptilian organization of limbs and feet they were able to attain so much larger size than has since been attained by the land mammals with their more perfected organization. Throughout the Cenozoic we see race after race of gigantic land mammals successively culminating and disappearing, each a little larger than its predecessor, each assuming the rectigrade limb as it approaches its maximum size, the Proboscideans, the latest and largest of all, and, so far as can be judged, the most perfect in mechanical organization. But the Sauropoda, away back in the Jurassic, far surpassed the largest elephants in size; and yet their joints are rough, imperfect, cartilage covered, their muscular attachments imperfectly differentiated. If the elephant is the largest size that the perfected mammalian organization permits, how is it possible that the relatively imperfect dinosaur organization could so far exceed it? And if it is not, why have none of the numerous gigantic Tertiary mammals exceeded this size?

If, indeed, we regard the Sauropoda as aquatic animals, adapted to wading, we solve this difficulty readily enough, and find also an explanation for various peculiarities in their construction which remain unexplained if they are considered as land animals. A wading animal has the greater part of its weight buoyed up by the water, and might attain a much larger size without transcending its mechanical limitations, just as the whales and some true fishes attain a much larger size than any land animal.

A second point that does not seem to have been brought out in the discussion is that the dinosaurs are distinguished from other reptiles by the relatively large size of the legs as compared with the body. In this respect they have the proportions of mammals and birds. The significance of this would seem obvious. A crocodile, turtle or lizard crawls habitually, because his legs are not large enough to carry the weight of his body. In dinosaurs, as in mammals and birds, the legs are large enough to carry the body comfortably clear of the ground and presumably served that purpose.

The nearest approach to the dinosaur proportions is seen in some of the lizards, and it is just among these that we find a tendency to lift the body from the ground, especially during running.

Another general consideration lies in the question of the primary adaptation of the dinosaurs. Dr. Hay very justly remarks that it is by no means necessary to suppose that the bird-like (bipedal) dinosaurs had passed through a mammal-like (quadrupedal) stage of evolution. Indeed, if we regard the lizard as illustrating early stages of a similar adaptation, the evidence would be just the other way; the bipedal stage in dinosaurs came first, the quadrupedal stage was a secondary adaptation. This is generally admitted as regards the quadrupedal dinosaurs of the Predentate group; the reviewer believes that it is also true of the Sauropoda, although the indications of former bipedalism are less apparent in this group. The hypothesis would serve, however, to explain several odd features in their construction—*e. g.*, the combination of everted elbow with straight knee—and would connect them more definitely with the Theropoda of the Triassic, to which they are structurally traceable, as von Huene has demonstrated.

SHORTER ARTICLES AND DISCUSSION

EVOLUTION WITHOUT ISOLATION

THIS is the title of a brief but interesting article by O. F. Cook, in the AMERICAN NATURALIST for November, 1908. My response to the same has been delayed by the pressure of other things.

I fully agree with Dr. Cook in his statement that "The choice of words is worthy of careful consideration, but words should not lead us away from the broader issue of biological facts."

We both maintain that there may be evolution without isolation; but I do not see how he can reconcile the following statements, found in the above mentioned article, with the facts of nature. "The separation of a species into two or more parts allows the parts to become different, but there is every reason to believe that evolutionary changes *of the same kind* would take place, if the species were not divided." Again: *"Isolation,* though making more species, *impedes evolution."* Does he mean that if man and the anthropoid apes had remained one freely intergenerating species, a higher degree of intelligence would have been reached than has been attained by man under the condition of isolation between him and the apes? Does he mean that the progress of the mammals, as a whole, would have been more rapid, if they had remained one constantly intergenerating species? Does he mean that, in the case of mammals, *"changes of the same kind,"* as we now see, in size, in form, in instincts, in power to live, some in the sea like the whales and the porpoises, some on the land, some on the trees, some in hand-made houses, would all have taken place, if we, the mammals, had remained one species? Would these changes have come in successive generations, in one continuously changing kaleidoscope; or would each successive generation have become increasingly complex, till the mouse could produce, not only mice, but all other mammalian forms, including the cat, the flying-squirrel and the whale?

In many places in my volume on "Evolution," published by the Carnegie Institution, I speak of isolation and selection as *controlling factors,* while growth, reproduction, heredity and variation are classed as fundamental conditions in evolution. Some of these passages will be found on pages 29–34, 59–60, 79–80, 138. I also show that the forms of isolation and selection, that divide and guide the process of evolution, are often determined by relations between sections of the species, and may therefore be classed as autonomic. See pp. 138–39, 141–44 and 158. These autonomic forms of isolation and selection come under what Dr. Cook defines as processes of evolution, that is "processes of spontaneous change," as does also the process of reproduction with variation. If autonomic processes of isolation and selection are forms of evolution, shall we claim that natural selection, because it relates to the power of individuals and groups to meet influences in the environment, has, therefore, nothing to do with evolution, except as it retards evolution? If the power to assimilate good and abundant food helps in the process of evolution, may not the survival of those having this power in the fullest measure help in the same process? How then can Dr. Cook say, as on the second page of his article, that isolation and selection neither cause evolution, nor help it along? I can suppose that his answer might be, that, in as far as these factors have influence, the changes produced cease to be spontaneous, and, therefore cease to be evolution, as he understands evolution. But this explanation does not seem to be applicable to cases of transformation arising under isolation and selection caused by autonomic influences, for example by sexual and social instincts.

There are, it seems to me, many difficulties in the way of regarding the term evolution as applicable only to "spontaneous processes of change," unless we class all vital action, including variation and the survival of the fittest, as spontaneous, in that it arises from within, and its origin is life producing life from itself, and never life springing out of the dead environment, or out of widely different forms of life. And then we should have to meet the objection that all life is dependent on external conditions for its food, and, therefore, for continued existence, and so no vital action is spontaneous in the sense that it is independent of conditions in the environment.

Let us suppose that a little snail, clinging to a leaf is carried by a bird, from the home of the species in a valley on this island of Oahu, and dropped in an adjoining valley half a mile away, where the conditions of soil, vegetation, rainfall and temperature are the same as in the home valley. It finds a grove of the same kind of trees as that from which it came, and from its young arises a permanent colony. At the end of a few scores of years, what do we find? It has blossomed out in a new group of variations not found in the original stock, and some of the original characters have disappeared. Here is what seems to be *"a spontaneous process of change";* and we are about to call it a genuine case of evolution, when Dr. Cook reminds us that, if this change could not have taken place without isolation, it is not spontaneous, and that it is really a case of the impeding of evolution.

In the course of time another branch colony is formed, which varies from the original stock in habits of feeding and seeking of shelter from the sun. It gradually, but spontaneously, takes to the shrubbery near the ground, and deserts the trees; and so subjects itself to a new form of selection. The change is greater than in the former case, and is undoubtedly due to spontaneous variation, with survival of the fittest under new conditions chosen for itself spontaneously; for the kind of trees, on which the original stock lived, are found in abundance all around. Shall we call the process a case of evolution, or simply the checking of evolution through isolation and selection? I am inclined to define evolution so as to include the processes of change in such cases as these.

In this same article we find statements giving still greater limitation to what the author considers the real process of evolution. In the last paragraph it is called, "The processes of spontaneous, progressive change in species." On the third page also, we read: "Divergence may be greater than evolution when changes are not progressive, but sideways, or backwards." If the change in a species must be shown to be entirely spontaneous, and also not sideways or backwards, but upward, before we can venture to speak of it as an example of evolution, this word, now so popular, will find itself badly ostracized. "Speciation" is introduced as a rival for part of the field; but I am not sure that it will show itself better fitted than the term *divergent evolution.* I am, however, willing that the fate of the two should be left to the struggle for existence, and the success of the fittest, which I regard as one of the controlling factors in the evolution of language. The statement I am unwilling to accept is that isolation and the survival of the fittest (that is species-formation), have no connection with evolution except that they may impede the process. If all organisms came from one original intergenerating stock, deriving its food from the inorganic world, and from the dead individuals of its own kind, how far could evolution have progressed without any formation of separate species? What would now become of the organic world if isolation and selection ceased and all the separate species were merged in one? When I say that there may be evolution without isolation I mean without *additional isolation*. I do not mean that the undoing of all the effects produced by vital forces making isolation complete, though the different genera occupy the same district, would be an advance step in evolution. On the contrary, I think that such an undoing would mean the crumbling of the whole fabric of the organic world.

Is not racial evolution a term that we can rightly and wisely apply to all the processes of change in organisms affecting characters that are subject to the laws of heredity and variation? May it not be applied to all changes in races and species resulting, not only from the action and reaction of members of the same species upon each other, but also from the action and reaction between individuals or groups and their environments? May not evolution be either divergent, convergent or parallel? either progressive, or retrogressive? May it not take place without any change in the environment, and in that sense be spontaneous; and may it not be due to vital action stimulated, guided, and controlled by external conditions?

HONOLULU, HAWAII. JOHN T. GULICK.

RETROACTIVE SELECTION[1]

IN his contribution to THE AMERICAN NATURALIST of July, Professor Marshall makes some statements which I wish to correct. Among other things he says:

---

[1] "Retroactive Selection" is a term used by me to designate the modifications of each selection by the selections which follow. Thus, selection No. 2 modifies selection No. 1 by eliminating part of the animals which selection No. 1 retained as breeders. Selection No. 3 modifies selection No. 2 by eliminating some of the animals which selection No. 2 retained, and this in turn causes a second modification in selection No. 1 by eliminating more of those originally retained. In the same way, selection No. 4 modifies selections Nos. 1, 2 and 3; selection No. 5 modifies selections Nos. 1, 2, 3 and 4; and so on.

A study of retroactive selection is a study of the successive modifications of early selections by the retroactive effect of later ones.

> Mr. Redfield would say that the effects of environment are inherited.

It would require too much space to explain how this misapprehension of my position became prevalent. It is sufficient for the present purposes to say that it is a misapprehension, and that I am not taking the ground that the effects of environment are inherited—at least not in any sense in which a plain statement to that effect would imply.

What I am interested in at the present time is learning what explanation others would give of certain facts which I have dug out of records. One of these facts relates to the ages of sires in pedigrees of 2:10 trotters, or trotters in general, and as this subject has already been opened it appears a fitting one to continue.

After quoting what I had to say about sires appearing older and older the further we go back in the best pedigrees, Professor Marshall says:

> The evident conclusion from this statement is that our best horses come from an increasing popularity of *younger* sires.

The error in this statement is more in what it implies than in what it actually says. Young sires are popular and have been popular during the entire history of breeding the trotter. Many very fast trotters have come from such sires, but a consideration of those raises a collateral question which it is better to postpone to a later date. What actually occurs in the breeding of trotters may be described as follows:

Assume some thousands of animals belonging to the trotting stock as it existed in this country, say seventy-five years ago. Using concrete numbers for illustration, we will say that out of these horses one thousand stallions are selected for breeding purposes to produce the next generation. We will designate these one thousand stallions as the first generation and the first selection in a process of selection which we will follow through several generations as it has actually been employed by the breeders of trotters. These one thousand stallions were sons of sires which were, on the average, 10.4 years old at the time the sons were born. It may be added here that this 10.4 years between generations in the male line is the approximate average as it has existed at all times within the known history of the trotter. A detailed investigation of the " Trotting Register " for different periods shows that at no time have ordinary breeding operations varied from this except in the value of the decimal.

The one thousand stallions of the first generation produce the second, of which some ten thousand or more are stud colts. Out of these a second selection of one thousand stallions is made for breeding purposes to produce the third generation. The stallions of this second selection are sons of sires averaging 10.4 years of age, and the selection is based principally upon the performances of their sisters, their cousins and their aunts. Don't fail to note the fact that until very recent years, stallions were rarely selected for breeding purposes because of their own performances. Horse history is full of the assertions by breeders that stallions intended for breeding should never be raced.

Now we come to the critical point to which close attention should be given. The one thousand stallions of the second selection are not the sons of the full one thousand stallions of the first selection—one son for each sire. On the contrary, some sires in the first selection are represented by numerous sons in the second selection, while other sires in the first selection are not represented at all. In other words, about one-half of the first selection of sires is cut out by the second selection. This weeding out of the sires of the first selection is done largely *after* the sires themselves are dead, and is based upon the performances of animals other than the sires of either generation.

When we examine the sires of the first selection after the weeding-out process involved in the second selection, we find the sires eliminated by the second selection to have been principally, though not wholly, sons of young sires; and that the sires which are retained to breed on in the male line to the third generation, are principally, though not wholly, sons of old sires. The net result of cutting off part of the original selection by the second selection is that the 500 left are sons of sires averaging about 12.5 years of age.

In due course of time a third selection of one thousand stallions is made from the third generation for the purpose of producing the fourth, and they in turn are sons of sires averaging 10.4 years of age. But all of the stallions of the second selection are not represented in the third selection. In fact about one half of them are cut off, with the result that the 500 which are left in the second selection, after making the third selection, are sons of sires averaging 12.5 years. Now, when the third selection cut off part of those originally in the second selection it also cut off many lines of descent back to the first generation. The horses which were thus cut out of the first selection by the third selection, occurring some thirty or more years later, were more largely sons of young sires than sons of old sires, with the net result that those left were sons of sires averaging 13.5 years of age.

This is the process which has been going on from generation to generation—each selection reducing the number of horses in earlier generations which are left to breed on to later generations. Chester proved some years ago that all known standard trotters were descended in the male line from one or another of no more than seventeen foundation horses. While these all stand as having been progenitors of trotters, the majority of them represent what are now extinct families, so that the trotters as now bred come in the male line from only six or eight horses.

The process set forth explains how it comes about that, in examining the pedigrees of any trotting stock, the further we go back in those pedigrees the older the sires appear, but it does not explain *why* a late selection cuts off young sires and preserves old sires of earlier generations.

That is the supreme question I am asking biologists. I have asked it in several forms before without getting a reply commensurate with what I consider the importance of the question. It is hoped that the present form, accompanied by the explanation upon which the form is based, will bring forth a genuine effort to explain *the cause* of these remarkable facts.

Casper L. Redfield.

THE LOGIC OF CHANCE IN PROBLEMS OF GENETICS

The literature at present appearing dealing with problems of genetics and evolution teems with uncertainty and inexactness in the use and misuse of the word "chance." Some definite understanding of the significance of the concept as a legitimate category of scientific reasoning seems desirable. At any mention of the word chance, some listener is sure to rise in protest with the old adage—"There is no chance, it's only your ignorance." The acceptance or the rejection of this bit of prophecy depends on the ultimate postulate of the absolute uniformity of nature. The truth of this postulate is a metaphysical question with which the ordinary student of genetics is not concerned. He is reminded of the fact that Darwin and all after him have used the word "chance" in many ways and he demands a definition of the term which shall meet his usage without involving metaphysical postulates.

The particular problem of genetics arises within a more or less precise universe of discourse. Within it lie a broad range of biological phenomena which the student of the problem is bound to take into consideration. Without this definite universe of discourse lie a still greater range of phenomena—chemical, physical, geological, etc.—which he is bound to neglect. His problem can not be made to encompass the whole universe, simply because the multiplicity of facts regarding the universe impede rather than advance the progress of the understanding of his particular problem. His universe of discourse must be precise and relatively small to be serviceable. Within this limitable universe of discourse the observer will discover certain regularities. These will constitute for him the laws. Certain other groups of phenomena will appear seemingly without regularities. These are chances. The reduction of chance to law will consist, ordinarily, of determining more facts regarding the chances and also in so extending the boundaries of the original universe of discourse that new and theretofore unobservable regularities will appear.

In problems of genetics the occurrence of an event said to be due to chance may be ascribed to two separate but independent sets of conditions. The internal conditions are those which are entirely confined to the original universe of discourse of the problem—as for instance, the conditions of the gametes in the chance union of a Mendelian hybrid. The external conditions are those which are not centered in the immediate elements. They are such as age, strength, and the like, of the gamete producing animals. Let ϕ represent the chance occurrence of any event, and let $a, b, c, \ldots$ represent a series of internal conditions either known or unknown, and let the coefficients $A, B, C, \ldots$, etc., represent the intensive value of a, b, c in determining the result. Similarly let m, n, o represent certain external conditions and M, N, O their coefficient of intensive value. Then the formula for the chance occurrence, ϕ, of an event becomes

$$\phi = f\ (Aa, Bb, Cc \ldots Mm, Nn, Oo \ldots)$$

As far as I can find in the recent literature of genetics the concept of chance has appeared with three different uses. It is used first to describe the degree of probability for the crossing of individuals which differ more or less from one another. In this sense one may say the chance of producing a cross varies with the relative distance of the individuals producing the gametes in the Linnean classification. The second use of chance is that concerned with the occurrence of a mutant in those theories of the origin of variation through mutation. In this sense one speaks of a mutant as a chance or sport variety. The third type of usage has grown up in the literature of Mendelian crossing and of sex determination according to the male and female producing spermatozoa of arthropods. In this third type of instances the chance is reduced to the occurrence of one of two events.

It is the purpose of the present note to apply the formula of chance as previously given to these three separate uses of the term.

1. Take, for example, the type of the first usage mentioned above—the chance of a cross between different varieties and different Linnean species. If ϕ represents the chance of a cross between any two individuals, then the occurrence of that cross is determined by a series of internal conditions a, b, c, etc., which rest entirely within the structure of the gamete, as for instance, the innate characters of the centrosomes or the chromosomes. These are entirely contained within the cell itself and are, therefore, independent of any external modification. It is they, in all probability, that determine the amount of cleavage of a zygot produced from the union of gametes from individuals of different species, as for instance, when the eggs of *Rana fusca* are fertilized by sperm of the *Triton,* but development stops suddenly after a few irregular cleavages. The logician would say that these internal factors represented the conditions contained within the original universe of discourse of the particular problem in question. The union is also determined by external conditions m, n, o, etc., which lie without the gametes, as for instance, the ripeness of the eggs, as shown by Hertwig in experiments on the sea-urchin, or by the presence of alkaline in the water, as given by Godlewski when he crossed the sea-urchin with a crinoid *Antedon.* These external conditions are those that lie without the original universe of discourse of the problem.

2. Take, as a second usage of chance, the chance production of

a mutant. Let ϕ represent again such a chance occurrence. Then ϕ is a function of a, b, c, certain difficultly understood conditions which seem to reside within particular gametes and produce a new variety, differing considerably from the parental forms. The various occurrence of mutants among domestic animals probably resulted from such internal conditions. The very light silver cat, Chinnie, made his appearance about 1878, and has been the stock ancestor from which all the line-bred silver cats have since been produced. No external factors determining the occurrence of this sport could be traced. DeVries, who, of course, emphasizes these chance occurrences of the mutants, seems to believe that the internal conditions are alone responsible for these chance variations, yet MacDougal is said to have produced mutants of the evening primrose by salt solutions. If this observation is borne out by subsequent investigation, such mutant-producing factors would be represented by m, n, o of our formula, the external conditions for the production of chance occurrence ϕ, in this case the mutant.

3. Lastly, the concept of chance is of frequent occurrence in Mendelian literature. The Mendelian formula for the production of generation F^{II} demands that the independent inheritable characters shall separate in the gametes of F^{I} and recombine according to the pure law of chance, and Mendel's work on peas bears this out to a remarkable degree of accuracy. Similarly if we believe that the sex of certain arthropods is determined by male and female producing spermatozoa, but the egg is neutral, we must assume that the determination of sex is purely a matter of the chance union of the male or the female producing spermatozoa with a neutral egg. Nor in this case is the formula of ϕ without its significance. The work on certain parthenogenetic forms shows that certain spermatozoa, those without the accessory chromosome, are degenerate and presumably non-functional. This degeneration is obviously an internal condition, a, of the formula, but since it is known that various sex ratios exist all the way from the approximate one to one of many of the mammals to the very disproportionate ratios, approaching parthenogenesis in the nematodes, it may be supposed that this internal degeneration of certain of the spermatozoa is itself the function of other and unknown variables. Again, the external conditions m, n, o, such as age, maturity, nutrition, etc., may also have an influence upon the chance occurrence of the sex-producing factor of the spermatozoa.

The formula has perhaps an advantage, therefore, in suggesting a definite usage of the concept of chance in these problems, and also of suggesting, what writers sometimes confuse, the marked difference between external and internal determining factors. It rests upon a definite logical issue. Every scientific problem arises in a more or less definite universe of discourse. The limits of this universe of discourse determine the possibility of discovering regularity among the experiences it defines. Such internal regularity gives law, its absence, chance. This definition, therefore, gives to chance a definite and precise meaning, capable of an exact usage in scientific enquiries. It does not involve the affirmation nor the denial of the ultimate uniformity of nature.

ARTHUR S. DEWING.

CAMBRIDGE.

NOTES AND LITERATURE

ANIMAL STRUCTURE AND HABITS

PROFESSOR R. HESSE and Professor F. Doflein have undertaken the preparation of a general work on the structure and habits of animals, of which the first volume[1] has just appeared. This volume deals in a most complete way with the animal as an independent organism and the authors reserve for subsequent treatment the consideration of animals in relation to their environment. After an introduction which deals with life, protoplasm, the cell, animals and plants, the theory of descent, etc., the subject matter of the volume follows in four books dealing with the statics and mechanics of the animal body, its metabolism, powers of reproduction and inheritance, and the nervous system and sense organs. A final section takes up the relation of the parts of the animal to the whole. As a sample of the thoroughness with which the subject is treated the contents of the first book may be taken. This part opens with an account of the shapes and movements of the unicellular animals followed by a consideration of these aspects of the multicellular forms. The skeleton in the invertebrates and vertebrates is fully described. The power of animals to float in water and in air is next considered, and the remainder of the book is given over to a presentation of locomotion proper. This includes movements by cilia and by muscles and under the head of muscular locomotion is considered locomotion by steps such as is seen in leeches, etc., by wriggling as seen in snakes, eels, etc., and by means of lever appendages. This last section includes swimming by appendages, springing, running, climbing and flying, and the last of these is discussed in relation to insects, bats and birds. The treatment is rich in examples and abounds in well-constructed diagrams and clear illustrations. The remaining sections of the book are equally full and exhaustive.

The subject matter, though often complicated, is treated in an unusually clear way and is free from unnecessary technicalities; in fact the treatment may be said to be popular in the best sense of the word. This perhaps is the reason the book has been set in Gothic instead of Roman type, a fact which will appeal to the average German reader, though perhaps not to those outside Germany. The material is thoroughly modern without, however, involving the reader in present-day disputed questions, and in some respects the volume may be looked upon as a rewriting of the ground covered by Bergmann and Leuckart's "Anatomisch-physiologisch Uebersicht des Tierreiches." To this work the author acknowledges much indebtedness and appropriately dedicates his volume to its authors. In the revival of interest in the study of form and function Professor Hesse's volume should find its place on the book shelf of every zoologist.

---

[1] "Tierbau und Tierleben in ihrem Zusammenhang betrachtet," von R. Hesse und F. Doflein, Band I., Der Tierkörper als selbständiger Organismus von R. Hesse. Leipzig und Berlin, B. G. Teubner, 1910, 8vo, xvii + 789 pp., 480 figs., 15 Taf.

G. H. Parker.

PLANT PHYSIOLOGY[1]

Dr. Kauffman has published a very interesting paper on the influence of various substances on the sexual and other characters of certain species of Saprolegniaceae. Thorough studies of this kind are likely to add much to our knowledge of the biology of the fungi and will eventually, no doubt, furnish a mass of data which may be of material aid in the solution of some of the fundamental problems of evolution and variation.

One notable advance made by the author is the use of pure cultures obtained from single zoospores. A very successful and apparently simple method of obtaining the single spore cultures is described. It consists in making dilutions of zoospores in sterile water and sprinkling them with a pipette on the surface of a gelatine plate where they can be located with the microscope, and when they have germinated, they may be transferred to other plates or tubes.

The author does not state how many generations of each organism were grown from the same original single zoospore culture under the same conditions. We infer from his account, however, that in most cases the transfers were made from portions of the mycelium or gemmæ and were in the nature of vegetative reproductions rather than new generations.

---

[1] "A Contribution to the Physiology of the Saprolegniaceæ, with Special Reference to the Variation of the Sexual Organs," C. H. Kauffman (*Annals of Botany*, No. 87, Vol. 22, p. 361, July, 1908).

We doubt whether some of the conclusions reached, in regard to the causal nature of the various chemicals used in the different cultures in producing oogonia and other changes in certain of the species studied, should be accepted without further study and more conclusive evidence. The author says: "The results so far indicated show that it is possible to produce, where hitherto they were believed to be absent, antheridial branches of the normal type known in other species of the family, and that their production is conditioned by the presence of definite inorganic salts." The fact that antheridial branches appeared quite constantly in cultures containing certain inorganic salts, does not, in our opinion, necessarily prove that their occurrence was due entirely to the action of such salts. In order to make such a conclusion justifiable, it would be necessary, at least, to carry on a very long series of cultures, covering many generations of pedigreed forms originating from different individuals of the organism under investigation, to say nothing of other possible factors which may be unknown. It seems probable from recent investigations by Miss Wakefield[2] and others that there are fertile and sterile races or strains of species which differ in no other respect from each other and apparently do not depend upon the presence of any particular inorganic salt. An organism reproduced vegetatively would also presumably tend to be more constant in its behavior and show less variation than when each new generation was produced from spores.

Our studies of pedigreed strains of many generations of *Glœosporium* and *Colletotrichum* started from single spores lead us to the conclusion that there are some other factors or forces involved in the variations which occur in different generations from single spores which have no perceivable connection, so far as yet determined, with the composition of the medium in which they grow. Apparently spontaneous variations appear in such series of generations at the most unexpected moment under apparently identical conditions of environment and culture media. We say apparently because it is probably beyond our power at present to determine much less to control all the factors concerned in the growth and behavior of an organism.

---

[2] Wakefield, E. M., "Die Bedingungen der Fruchtkorperbildung bei Hymenomyceten, sowie das Aufftreten fertiler und steriler Stamme bei denselben," *Naturwis. Zeitschrift fur Forst- und Landwirtschaft*, 7. Jahrgang, 1909, 11 Heft, pp. 521–551, 1909.

Some series of cultures which produce no oogonia are believed by the author to possess a distinct physiological character in this respect, whereby they can be readily separated from series which produce oogonia. If these organisms obey the same general laws as those with which we have been working, it would be injudicious, at least, to say positively that they do not produce oogonia without having grown them for many generations and from different individuals of the same origin.

The idea, that the same conditions of nutrition, temperature and general environment always produce the same results upon the individuals of a species of organism, has, we believe, as yet no sufficient basis in demonstrated fact. The suggestion of the author, that a standard for the measurement of species comparable to the standards used in physics and chemistry, can be devised, is, we fear, a delusion and indicates a failure to recognize the apparently fundamental fact of biology that organisms possess inherent tendencies or forces which may enable them to vary without necessary dependence on any particular nutritive substance or environmental condition which can be at present definitely determined. The causes of these variations or mutations may perhaps be determined when we are able to recognize, analyze, measure and control all the numerous delicate complex factors concerned, many of which are now probably beyond us and not even surmised.

At another point essentially the same solution of the ever-vexing and recurring species question is given as follows: "At first thought this seems to indicate that no separation can be made of the different species of Saprolegniaceæ by means of constant characters. We can, however, use the resources of the chemist and physicist, and, by stating the exact conditions of culture establish a standard to which all forms may be referred." It is further stated: "It would seem necessary, then, in monographing such a family as the Saprolegniaceæ to refer all the species to definite conditions, which should be uniform for all, and to determine in each case the variability to the extreme attainable limits." If it were practicable to apply such a test, there is apparently little to justify the expectation that it would prove satisfactory. That mutations or variations may be induced or brought into expression by changes in conditions or other stimuli, is probably true, but to determine among the multiplicity and obscurity of the factors in any particular case, just what these conditions or stimuli are, is exceedingly difficult, even though we assume in the beginning that the organism under investigation has no latent hereditary possibilities of change indirectly or not at all dependent upon its immediate environment.

Our work with *Glœosporium* and *Colletotrichum*, part of which is yet unpublished, indicates that so far as these organisms are concerned, at least, no such method would prove practicable; as the same organism, so far as any morphological characters or host relations serve to identify it, will frequently behave very differently when cultures of the organism obtained from different acervuli on leaves of the same host are made. This fact might be easily explained, perhaps, by the assertion that such forms are the elementary species of DeVries and others, or races or strains, but this rather complicates than simplifies the problem. If there are numerous elementary species of the same fungus to be found on the same host without recognizable morphological differences, it is certainly questionable whether any practical taxonomic work could be founded upon such a basis. Until it can be demonstrated that an organism is entirely controlled by its external environment and nutritive conditions and all its hereditary expressed and latent characters are known, it will be hazardous to base positive conclusions upon such data. We must continually keep in mind and be prepared to make allowance for the inherent hereditary characteristics and possibilities of the organism which may possibly find expression in any particular individual or generation.

The vast and complex problems of determining the origin and cause of the form and behavior of even the simplest living organism is not perhaps to be so easily solved. The more it is studied the more difficult it appears. All exact knowledge and data in regard to these phenomena are to be welcomed, however, and the more we come to appreciate the difficulties of the subject the better able we should be to devise experiments that will yield the necessary data which may eventually reveal to our finite minds some of these profound mysteries of nature.

C. L. Shear.

Methods in Plant Histology

By CHARLES J. CHAMBERLAIN

Second edition, revised and much enlarged; 272 pages, with 88 illustrations, 8vo, cloth; net $2.25, postpaid $2.39

THE first complete manual to be published on the subject of botanical microtechnique. It contains detailed directions for collecting and preparing plant material for microscopic investigation, setting forth the advantages and disadvantages of the different methods.

Will no doubt find a place in every well-regulated library, and will be found very useful by private students.—*Plant World.*

It is an excellent book for the individual worker and for classes in colleges.—*Education.*

A Laboratory Guide in Bacteriology

By PAUL G. HEINEMANN

158 pages, interleaved, with 37 illustrations, 12mo, cloth; net $1.50, postpaid $1.61

A CLEAR and concise presentation of bacteriological technique, designed principally as a manual for the medical student, but highly useful also as a reference book for the biological teacher and investigator, as well as for practical workers in the fields of medicine and hygiene.

The instruction given is clear and accurate, and the practical exercises are well selected.—*The Lancet* (London).

A book such as this must facilitate very greatly the practical class work, for which it is most excellently adapted. — *American Journal of Medical Sciences.*

The directions are clear and concise, and every stage is described so carefully that it is hard to see how the student can go astray. Physicians who are rusty in bacteriology cannot do better than buy this little book. The book is beautifully printed and bound.—*American Journal of Clinical Medicine.*

Animal Micrology:

Practical Exercises in Microscopical Methods

By MICHAEL F. GUYER

250 pages, 8vo, cloth; net $1.75, postpaid $1.88

THE title of this book will explain its scope. It is intended as a laboratory manual for textbook use. Its aim is to introduce the student to the technique of microscopic anatomy and embryology, emphasizing details of procedure rather than descriptions of reagents or apparatus. Sufficient account of the theoretical side of microscopy is given to enable the student to get satisfactory results from his microscope.

The directions are simple, explicit, and complete.—*American Journal of Clinical Medicine.*

The medical student will find it very useful as a guide to microscopic work.—*Journal of the American Medical Association.*

This is one of the cleanest works on microscopical technique we have ever seen, and is especially suitable for the beginner. It is full of points, tricks of technique not mentioned in other works, and is one that every student and physician should have.—*Medical Century.*

This valuable book is strong through its rigid exclusion of the trite and the conflicting. It is lucid and helpful, because a man long practiced in practical work has given what he believes the most expeditious and reliable method of obtaining a definite and comprehensive result. — *Medical Notes and Queries.*

A concise, eminently practical, and well-classified treatment.—*Science.*

The expositions of the methods recommended are admirably clear.—*Nature.*

One of the best and most practical works upon microscopic technique with which we are acquainted.—*American Naturalist.*

As a textbook it can hardly be improved. The research worker will find in this book just the information he frequently needs in preparing material with which he is not familiar.—*School Review.*

It does present in very clear form a judicious selection of methods, including an excellent untechnical account of the microscope and its optical principles, adequate for the undergraduate course in histology.— *Journal of Comparative Neurology and Psychology.*

ADDRESS DEPT. 33

Chicago THE UNIVERSITY OF CHICAGO PRESS New York

Cast of Head of Mummied Woman of the "Basket People" (Cliff Dwellers)

This is the specimen which Professor H. H. Wilder restored to approximately its normal contours by treating with a potash solution, as described in the American Anthropologist, Vol. 6, No. 1, Jan.-Mch., 1904.

The restored subject has been molded and cast in our laboratory. The head is tinted and is mounted upright on a black pedestal with incised label. Professor Harris writes:—"I have been out of town for a few days and on returning found what I consider a most successful rendering of my 'restored' Cliff Dweller lady, and wish to thank you heartily for attempting so difficult a task."

This head or bust is, perhaps, *the only authentic likeness of a prehistoric American in existence.* Copies, securely boxed, each........................ ....$ 8.00

We can also supply the following casts, all colored after nature.

HOMO SAPIENS

Skull of Engis Man, restored portions indicated..............................Price,	$2.00
Skull and Mandible of Cro-Magnon No. 1 (capacity much above the present average)...Price,	$4.00
Cranium of Cro-Magnon No. 2..Price,	$3.00
Cranium of Australian..Price,	$2.75
Cranium of Hottentot (recent)..Price,	$2.75
Series of brains of ten races of man (intercranial casts) from the Royal College of Surgeons. Casts are alabaster, coated with stearine. Each brain has its individual pedestal and label..............Price, set of ten,	$25.00

HOMO PRIMIGENIUS

Neanderthal Man, cranium and portions of skeleton (2 femora, 2 humeri, 1 radius, 2 ulnæ, 1 acetabulum, 1 scapula, 1 clavicle), together with intercranial cast.........Price, 12 pieces, $14, Skull or Brain, each,	$2.00
To facilitate the study of the anatomical peculiarities of this skull, a reprint of Professor Shaaffhausen's original description, now long out of print, is included.	
Man of Spy No. 1 includes calvarium, lower jaw, right sup. max., portions of clavicle and humerus, left radius, head of left ulna, right femur, and left tibia and patella ....Price,	$11.00
Man of Spy No. 2 : Calvarium, portions of left femur, right humerus, radius ulna and tibia...................................	$7.50
Skull only of Spy No. 1 or No. 2..........................	$1.75
Cranium and mandible of Homo neanderthaloides, Pohlig, Brunn..............	$4.00
Brunn—Cranium No. 2..	$3.00

PRE-HUMAN REMAINS

Mesopithecus pentelici, male cranium	$1.50
Mesopithecus pentelici, female cranium and mandible from the Pliocene, Pikermi, Greece	$2.00
Dryopithecus fontani, lower jaw on pedestal (Type-specimen of this large anthropoid from the fresh-water Miocene of Southern France).........	$2.25
Paedopithex rhenandus, femur, Pilocene, Eppelsheim, Germany..................	$1.25
Pithecanthropus erectus, cranium. Pliocene of Java.............................	$3.00

An 8-page illustrated description by the late Professor Marsh accompanies this remarkable skull. We fill orders promptly.

ANATOMICAL LABORATORY OF CHARLES H. WARD

"THE LENNOX," WEST AVENUE **ROCHESTER, N. Y.**

VOL. XLIV, NO. 526 OCTOBER, 1910

THE
AMERICAN
NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. **Variations in Urosalpinx.** Dr. HERBERT EUGENE WALTER - - - - 577

II. **Nuclear Phenomena of Sexual Reproduction in Gymnosperms.** CHARLES J. CHAMBERLAIN - - - - - - - - - - - - 595

III. **Nuclear Phenomena of Sexual Reproduction in Angiosperms.** Professor D. M. MOTTIER - - - - - - - - - - - - 604

IV. **Shorter Articles and Discussion:** Sterility, Dr. MAX MORSE - - - - 624

V. **Notes and Literature:** Notes on Ichthyology President, DAVID STARR JORDAN. The Mammals of Colorado, Professor T. D. A. COCKERELL - - - - 634

THE SCIENCE PRESS

LANCASTER, PA. **GARRISON, N. Y.**

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. **Garrison, N. Y.**

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

THE BULLETIN—For bargains in Ethnolographical and Pre-historic Specimens. Books on Natural History, Science, Travel, Voyages, etc. See THE BULLETIN post free for 3 cent stamp.

4 Duke St., Adelphi—London—England

NATURE BOOKS

FRANKLIN BOOKSHOP

S. N. RHOADS, Prop.

920 Walnut St. Philadelphia

Second-hand Books Relating to Natural History.

Write for New Catalog.

Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

Henry Holt & Company

34 West 33d St., New York
378 Wabash Ave., Chicago

Microscopes and Accessories

Hand Cameras of Highest Quality

Binoculars, Prism and Galilean

the best obtainable for Nature Study

Scientific Instruments

Laboratory Apparatus

Max Meyer 18 West 27th St. New York

"Quality, Prices, Service Right."

THE
AMERICAN NATURALIST

Vol. XLIV | *October, 1910* | No. 526

VARIATIONS IN UROSALPINX

DR. HERBERT EUGENE WALTER
Brown University

1. *Introduction.*—In a paper which appeared in 1898 Bumpus[1] showed that, in the case of *Littorina littorea,* an introduced species shows more variability than the same species in its original habitat. This *Littorina* was recently so rare on the Atlantic coast that two pioneer specimens were reported by Verrill from Woods Hole in 1875 while the first specimen found at New Haven was in 1880. Twenty years later it was probably the commonest mollusk to be found along the new England coast and its range extended northward and southward considerably beyond this area. Three lots of 1,000 each, representing the former habitat of the species, were obtained from the coasts of Wales, Scotland and England, respectively, and these shells were measured so as to get an index of their variability. Then ten 1,000-lots of the introduced American shells were collected and measured for comparison and it was found that nowhere in any of the ten different localities, which extended from the St. Croix River in Maine to Newport, R. I., could shells be found that did not have a greater index of variability than did the British shells. Duncker[2] working over

---

[1] Bumpus, H. C., 1898, "The Variations and Mutations of the Introduced Littorina," *Zool. Bul.,* Vol. I, pp. 247–259.

[2] Duncker, G., 1898, "Bemerkung zu dem Aufsatz von H. C. Bumpus: The Variations and Mutations of the Introduced Littorina," *Biol. Centralbl.,* Bd. 18, pp. 569–573.

Bumpus's data afterwards by the most approved technical methods, confirmed his conclusion.

The oyster-borer, *Urosalpinx cinereus* Say, offers an additional opportunity to test the relative variability of a species when introduced into a new environment as compared with the same species living in the original habitat. This mollusk is a native of the Atlantic coast, living particularly on the oyster beds, where it causes considerable damage. In 1871 Mr. A. Booth, of Chicago, first transplanted the Atlantic oysters to the Pacific coast where, with varying success, they have since been maintained. Two lots of these shells were obtained from the San Francisco beds in 1898 and it was the original purpose of this paper to compare these introduced California shells with individuals from the Atlantic coast whence they were emigrated.

The work was principally done at the Woods Hole research laboratory of the U. S. Fisheries Bureau and I wish hereby to acknowledge the many courtesies received from the officers connected with that bureau, and particularly to express my indebtedness to Professor Bumpus who suggested the original problem. I wish also here to thank the following persons for aid in obtaining specimens: Dr. Bumpus for 1,500 California shells; Dr. H. M. Smith for 1,700 from Prince's Bay, Staten Island; Mr. G. W. Hunter, for 1,000 from Norwalk Harbor, Ct.; Miss M. E. Smallwood for 1,000 from Cold Spring Harbor, Long Island; Mr. C. T. Brues and Mr. A. L. Melander for 8,000 from Woods Hole, Mass., in 1902 and 1903; and Mr. C. S. Bennett for 4,000 from Woods Hole in 1908. Finally, I am particularly under obligation to Dr. J. Arthur Harris, who very kindly passed the manuscript under his statistical eye. It should be added that while Dr. Harris is responsible for much that does not appear he is in no way committed to what remains.

2. *Methods.*—In collecting, only living specimens were taken, thus eliminating beach-worn shells, and collecting was always done "systematically at random" (Daven-

port) so that any lot would, as far as possible, be typically representative of its locality. Lots of 1,000 were taken and shells not immediately measured were simply preserved in formalin until opportunity for making use of them arose.

In ascertaining statistically the variability of any lot of shells it was necessary to select for measurement two easily definable dimensions common to every shell and take the ratio of these two dimensions for reasons which will directly appear. The dimensions selected were the total height of the shell (*a* to *b*, Fig. 1) and the greatest dimension of the shell-aperture (*a* to *c*, Fig. 1). It was possible to determine these standards on *Urosalpinx* by the use of calipers with a considerable degree of accuracy. Any other dimensions which would lend themselves equally well to accurate measurement would have served quite as well to establish a criterion from which a comparison of variability in different lots of shells could be computed, since it was the *fact* of variation, and not the direction or character of it that was the object of the inquiry. The ratio of the two dimensions was used instead of a single dimension in order to eliminate as far as possible heterogeneity referable directly to growth. Had height alone, for instance, been used then groups of shells would be related to each other with reference to their variations in size or age only, and all that could be said in comparing lots from two localities would be that those in one locality averaged taller or shorter, and presumably, therefore, were older or younger than those from another locality. This would not be a suitable index for variation in form. On the other hand, when the ratio of two dimensions is taken, then the factor of absolute

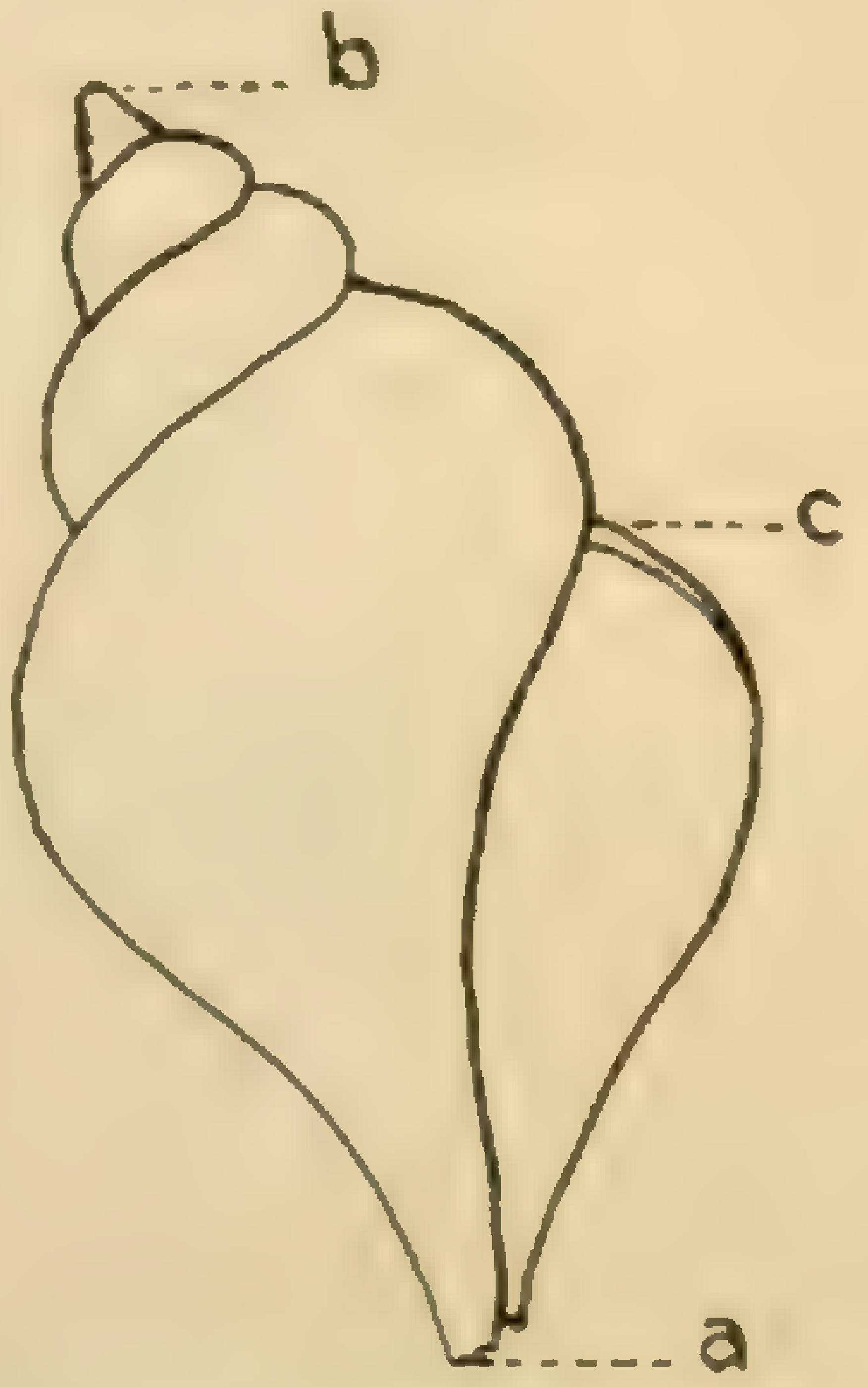


FIG. 1. *a b* = height of shell, *a–c* = greatest mouth aperture.

size is eliminated, while the factor of form remains. Thus a shell 20 mm. high with a greatest shell-aperture of 12 mm. would fall in the 60 per cent. class (20 : 12 = 60 per cent.), as would also a smaller shell 15 mm. high with a greatest shell aperture of 9 mm. (15 : 9 = 60 per cent.), while shells of the same height as the first, but with a 14 mm. greatest shell aperture, would rightly represent a variation in form since they fall into a different (70 per cent.) class (20 : 14 = 70 per cent.). This distinction may be more apparent by reference to Fig. 2 where

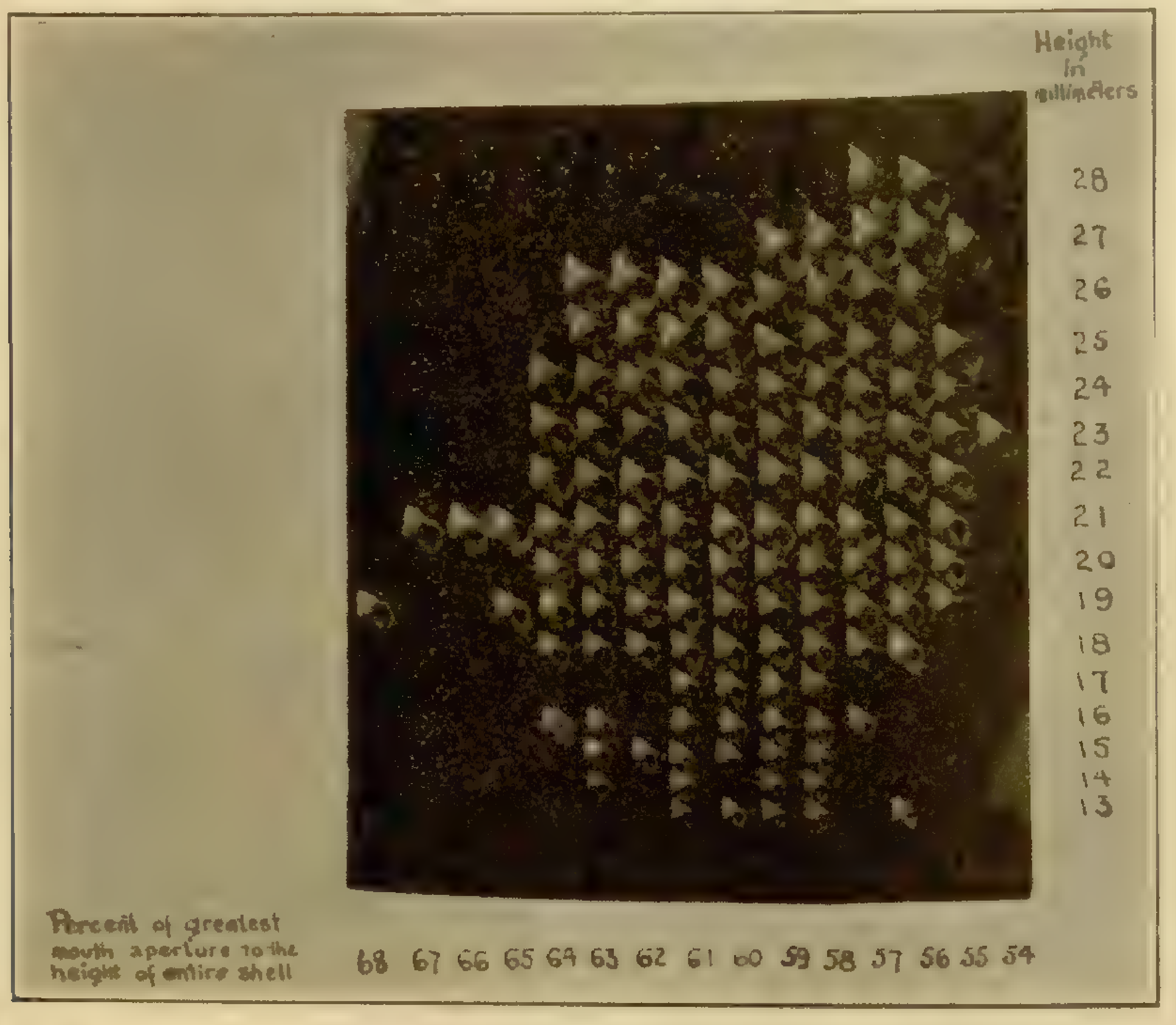

Height in millimeters
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
Percent of greatest mouth aperture to the height of entire shell
68 67 66 65 64 63 62 61 60 59 58 57 56 55 54

FIG. 2. The different classes of variants occurring in a specimen lot of one thousand shells to show how size, or the factor of growth, was eliminated in classifying the variants. The shells in the vertical lines all in the *same* percentage class, although their size (height) differs. The shells in the horizontal lines are in *different* percentage classes, although their size (height) is alike.

single representatives of all the different classes of variants that appeared in a certain thousand-lot of shells are arranged to show this point. Here the shells in any horizontal row are the same height, and have, therefore, presumably reached the same stage of growth, but at the same time they are all unlike in form since those at the left have larger "greatest shell apertures" than those at the right. On the contrary, all the shells in any vertical row, although varying in size, fall into a single form-group as determined by the ratio between total height and the greatest shell-aperture. A measuring machine such as that used by Bumpus for his work on *Littorina* made it possible to read the ratio of the two dimensions directly from a graduated arm without trouble of computation, thus greatly lessening the tediousness in obtaining the data.

3. *Are Variation Curves of any Locality Distinctive for that Locality?*—Tests were first made to ascertain how far the personal element in making the measurements could affect the results, since judgment in the use of calipers and in the manipulation of the measuring machine are by no means invariable factors. One such test, which is typical of several which were made, is shown in Table I, where the same lot of shells was twice measured.

TABLE I

THE SAME LOT OF A THOUSAND SHELLS TWICE MEASURED TO SHOW AMOUNT OF ERROR IN MANIPULATION.

Percentage Class.	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	Arithmetical Mean.	Standard[3] Deviation.	Probable[3] Error.
First measuring	1	2	2	5	28	58	118	185	182	171	139	49	38	15	5	2	62.101	1.992	±.0300
Second measuring		2	2	4	25	66	128	182	179	176	120	59	33	18	4	2	62.071	2.088	±.0314
Difference																	.030	.096	

The numbers ought to be identical. Their deviation from exact similarity represents the imperfections of manipulation and it will be seen that according to this test a difference of .096 in the standard deviation with a probable error of about ± .03 may be regarded due to imperfect technique.

Now in order to test whether the variation is characteristic and constant for any locality whence the shells came, two 1,000-lots were gathered on the same day in 1898 from the same restricted group of rocks on Nobska Point, Woods Hole, by no means thereby exhausting the supply. The figures for these two lots are shown together in Table II.

TABLE II

Two Lots of Shells of One Thousand Each Taken from the Same Rocks at the Same Time to Show the Probable Validity of Place-Modes.

Percentage Class.	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	A. M.	σ	P. E.
First lot		2	3	20	40	80	150	149	196	157	112	57	21	10	4	1	61.737	2.152	.0323
Second lot	2	2	31	14	61	79	144	148	185	160	106	55	25	10	7		61.694	2.234	.0336
																Difference	.043	.082	

The close resemblance of these two lots, which show a difference in standard deviation (.082) less than that shown when the same lot is measured twice (.096) as just indicated in Table I, warranted confidence in the probability that all the shells from a given place, when collected at the same time, exhibit the same characteristic sort of variation which may therefore be regarded as distinctive for that particular locality. Furthermore, a glance at Table III will show how widely the shells of various localities may differ with regard to the character and degree of their variability, a fact that assures us that in *Urosalpinx* we are dealing with a form whose variation is considerable enough to furnish favorable material for quantitative treatment.

---

[3] Formulas for standard deviation and probable error of standard deviation are found in Davenport's Statistical Methods (Davenport, C. B., 1899), as follows:

$$\text{Standard deviation} = \frac{\text{Sum of}\sqrt{[(\text{deviation of class from mean})^2 \times \text{frequency of class}]}}{\text{Number of variates}} \quad \text{or}$$

$$\frac{\Sigma\sqrt{(x^2 \cdot f)}}{n}$$

Probable error of standard deviation =

$$\pm 0.6745 \frac{\text{Standard deviation}}{\sqrt{2} \times \text{number of variates}} \text{ or P. E.} = \pm 0.6745 \frac{\sigma}{\sqrt{2n}}$$

TABLE III

Two Lots of Shells of One Thousand Each to Show Extremes of Variation.

Percentage Class.	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Devil's Foot	1	0	2	6	22	38	99	144	193	217	163	73	25	14
Prince's Bay						4	5	9	36	45	65	79	132	84
Percentage Class.	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**A. M.**	**σ**	**P. E.**	
Devil's Foot	3										58.358	1.849	.0279	
Prince's Bay	83	117	75	88	83	42	33	15	2	1	63.976	3.407	.0514	
										Difference	5.618	1.558		

4. *A Comparison of Atlantic with Pacific Shells.*—In the summer of 1898, following the method employed by Bumpus with *Littorina,* 7,006 *Urosalpinx* shells from various localities near Woods Hole were obtained and measured, with which were compared 1,528 introduced shells from two localities in California. From Table IV, in which these data are brought together, it will be seen that Bumpus's work on *Littorina* is apparently confirmed, that is, there is more variability in the introduced than in the endemic form, although the margin of probable error permits an overlapping in some instances.

TABLE IV

Atlantic and Pacific Shells Compared.

Locality.		Number of Shells.	A. M.	σ	P. E.
Woods Hole	West Shore	1,001	58.928	2.339	±.0352
	Penzance Point	1,002	61.718	2.737	±.0412
	Nobska Point	1,002	61.737	2.152	±.0324
	Nobska Point	1,001	61.944	2.234	±.0337
	Nobska Point	496	66.944	2.366	±.0507
	Barnacle Beach	998	63.932	2.604	±.0393
	Big Wepecket	1,006	57.426	2.052	±.0308
	Mid Wepecket	500	57.606	2.098	±.0447
Average			61.066	2.335	±.0386
California	Belmont Beds	1,008	59.051	3.023	±.0454
	San Francisco Bay	220	60.892	3.361	±.0703
Average			59.664	3.138	±.0538
Difference				.803	

5. *Shells from Buzzard's Bay and Vineyard Sound Compared.*—For the sake of scientific peace of mind the

incident should have been closed at this point, but uncertainty as to the degree in which the element of time took part in influencing the place-modes of variability led to the examination during the following summer of several thousand more shells. Four convenient localities near Woods Hole (see Fig. 3) where *Urosalpinx* was abundant were selected and three lots of 1,000 each were collected from each of these localities at intervals of two weeks apart. The data obtained from these shells is arranged in Table V.

TABLE V

Woods Hole Shells Arranged to Show Place Variation After Two Weeks Intervals of Time.

Locality.		Time when Collected.	Number of Shells.	A. M.	σ	P. E.
Buzzard's Bay	West Shore	July 5	1,000	58.669	2.137	±.0322
		July 21	1,000	59.598	2.211	±.0333
		Aug. 5	920	60.308	2.211	±.0323
		Average		59.503		
	Penzance Point	July 5	986	58.458	2.137	±.0304
		July 21	1,000	58.030	2.135	±.0322
		Aug. 5	1,000	60.308	1.982	±.0323
		Average		58.888		
Vineyard Sound	Nobska Point	July 5	1,000	62.085	2.040	±.0307
		July 21	1,000	62.690	2.172	±.0327
		Aug. 5	1,005	64.022	2.312	±.0347
		Average		62.934		
	Barnacle Beach	July 5	1,036	60.978	2.093	±.0310
		July 21	1,001	61.925	2.119	±.0319
		Aug. 5	1,001	63.281	2.186	±.0329
		Average		62.048		

From Table V it will be seen that in each of the four localities the arithmetical mean (A.M.) increased steadily, except for the Penzance Point—July 21—lot of shells. This general increase may be due to the fact that, as the season advanced, there were fewer young shells in any 1,000 lot. The young are produced in May and June from individuals that have wintered over, so that early in July the *Urosalpinx* community is made up of old adults from the preceding year and of young of various sizes. A month later the population is more uniform,

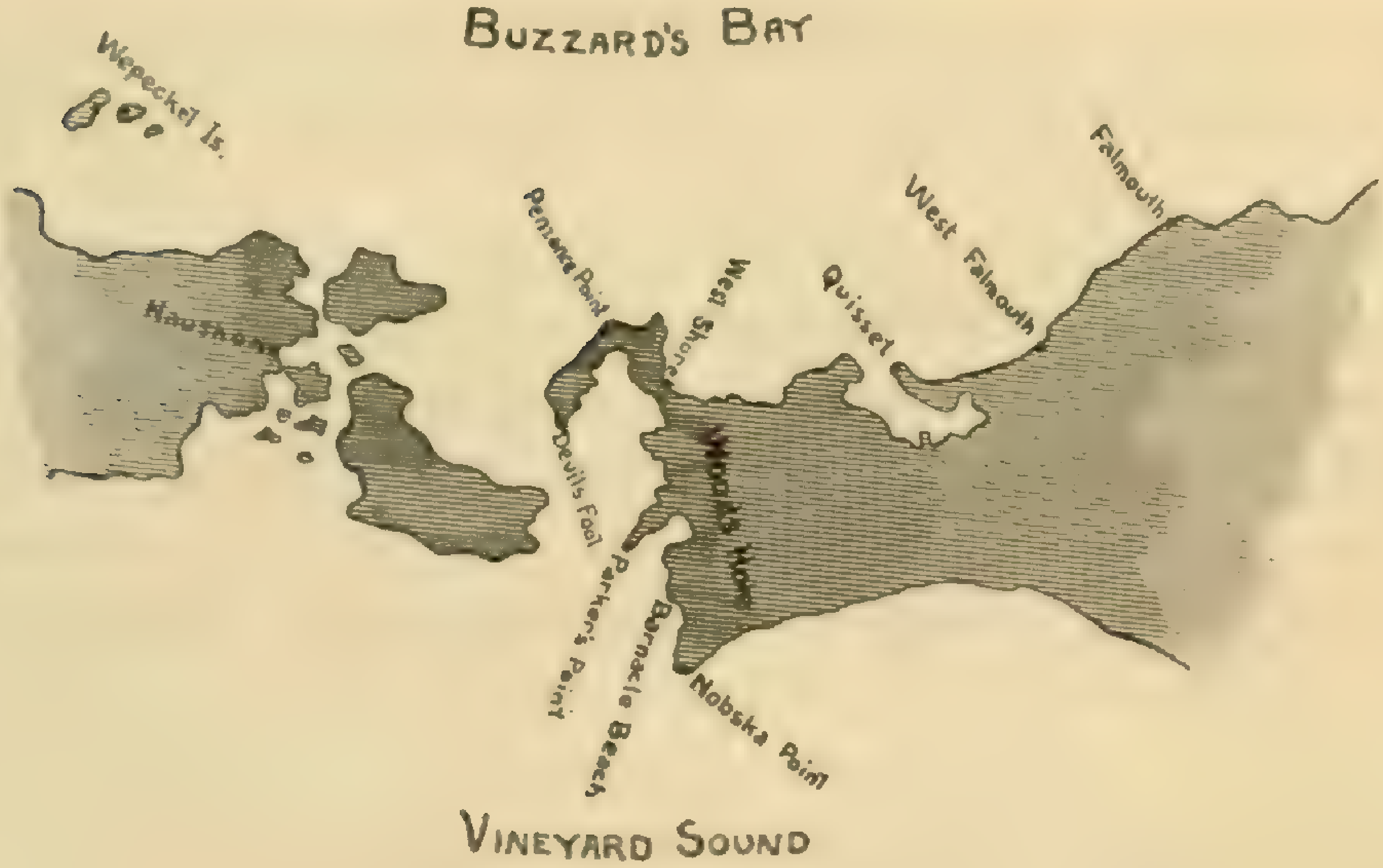

Buzzard's Bay
Wepeckel Is.
Naushon
Penzance Point
West Shore
Quisset
West Falmouth
Falmouth
Woods Hole
Devils Foot
Parker's Point
Barnacle Beach
Nobska Point
Vineyard Sound

Fig. 3.

due to the rapid growth and approaching maturity of the young ones. That the ratio of the two dimensions used changes somewhat with age is shown in a later table (Table VII), a fact that somewhat complicates a comparison between shells of any two localities. It will furthermore be observed that the variability of the Vineyard Sound shells as indicated by their standard deviation increases steadily from July 5 to August 5, reaching its maximum upon the latter date, but that for both the Buzzard's Bay localities the same is not true; on the contrary, in the case of Penzance Point the August 5 collections showed the *least* variability of any time. The fact that the maximum of the shifting seasonal variation does not occur at the same time in localities almost within sight of each other, as in the present instance, plainly indicates that comparisons of variabilities based upon the time-factor alone do not take everything into consideration. The shells from Buzzard's Bay range in their arithmetical mean from 58.030 to 60.308 while those from Vineyard Sound, separated from the former only by the narrow tongue of land on which the village of Woods Hole is located, form a distinct class ranging from 60.978 to 64.022. Here is a distinct place difference in the shells of the two general localities in question.

Shells obtained from other localities in Buzzard's Bay and Vineyard Sound conform quite closely with respect to their arithmetical means to the standards above mentioned.

6. *Time and Place Factors Compared.*—When a comparison of the standard deviation of these 1899 shells is made to ascertain whether the greater variability is associated with time (due to inherent germinal modifications), or with place (associated with environmental modifications), it appears that while time is rather the more important factor, yet the result is not uniform and convincing. This comparison is shown in Table VI, in which the difference between the standard deviation of the July shells of each locality with the July 5 shells of three other localities is obtained to indicate differences due to place, and second, the difference between standard deviation of the July 5 shells in each locality and those of July 21 and August 5 for the corresponding locality are reckoned to show the effect of time.

TABLE VI

A Comparison of the Differences in the Standard Deviation Variability of the 1899 Woods Hole Shells Arranged According to the Place-factor and the Time-factor.

Place Differences (July 5).				Time Differences.		
Nobska Point.	West Shore.	Penzance Point.	Barnacle Beach.	July 5.	July 21.	August 5.
—	.097	.025	.053	Nobska Point	.132	.272
.097	—	.122	.044	West Shore	.074	.080
.025	.122	—	.078	Penzance Point	.120	.033
.053	.044	.078	—	Penzance Beach	.026	.093
.058	.088	.075	.058	Average	.088	.119

In Table VI, if we first consider the case of the Nobska Point shells in the top line of the table and utilize those collected upon July 5 as a standard for comparison it appears that shells from the same locality but collected two and four weeks later show a greater difference in variability (standard deviation) than shells collected from any of the three other neighboring localities upon the same date of July 5. That is, the factors dependent upon time play a greater part in determining the amount of variability than do the factors dependent upon place. Furthermore, there is a greater difference of variability after four weeks (.272) than after two weeks (.132) have elapsed, just as would be expected if a progressive time change is taking place. The same general result appears also when an average of the four localities is reckoned, as shown in the bottom line of the table, but an examination of the second, third and fourth lines of the table reveals several instances in detail of non-conformity to this apparently general conclusion that time has more to do with determining variability than place. It is apparently safe to conclude, however, that the factors dependent upon time are at least as important, if not demonstrably more so, than those dependent upon space or locality.

TABLE VII

WOODS HOLE SHELLS ARRANGED ACCORDING TO THEIR SIZE.

Height in mm.	Actual No. of Shells.	A. M. Per Cent.	σ	P. E.
11	96	64.070	3.487	± .1753
12	139	63.911	3.558	± .1445
13	252	63.372	3.465	± .1049
14	341	62.983	3.954	± .1029
15	524	62.940	3.602	± .0755
16	866	61.960	3.020	± .0489
17	1,296	61.595	3.146	± .0417
18	2,033	61.171	3.124	± .0325
19	2,328	60.913	3.143	± .0311
20	3,366	61.004	3.209	± .0227
21	4,404	60.914	3.056	± .0219
22	4,807	60.739	3.122	± .0213
23	3,836	60.507	2.881	± .0222
24	2,854	60.171	2.951	± .0276
25	1,782	59.856	2.943	± .0322
26	949	59.706	2.663	± .0412
27	539	59.520	2.704	± .0555
28	239	59.213	2.520	± .0777
29	109	59.654	2.907	± .1328
30	63	59.305	2.740	± .1646
31	30	58.334	2.182	± .2455
32	23	58.665	1.916	± .1905
33	6	58.332	4.015	± .7818
34	12	59.083	3.009	± .4141
35	5	57.600	2.059	± .4392
36	3	60.000	8.185	±2.2554
37	1	54.000		
Total	30,903			

7. *Variations due to Age.*—It is indeed true that as the snail grows older not only is there a change in the total height of the shell, as would be expected, but also the ratio of the largest shell-aperture to the height diminishes in a definite way and the standard deviation becomes generally less. In other words, the older the shell becomes the less is the relative size of the largest shell-aperture to the total height and the less does it tend to deviate from the arithmetical mean. In Table VII the total number of shells measured in 1898, 1899, 1900 are arranged according to their height to illustrate this fact.

8. *Staten Island and California Shells Compared.*—In 1900 shells were obtained from several additional localities, among which were 1,665 from oyster beds on Prince's Bay, Staten Island. This lot of shells has a special interest because it was from this particular locality, according to Dr. H. M. Smith, of the U. S. Fish Commission, that the oysters, and accidentally with them the *Urosalpinx*, were obtained for transplanting to San Francisco in 1871. A comparison of the Staten Island shells with the California shells appears in Table VIII.

TABLE VIII

A Comparison of California Shells with those from Staten Island.

	No.	A. M.	σ	P. E.
California	1,528	59.741	3.286	±.0398
Staten Island	1,664	63.166	3.508	±.0412

From this table one of three conclusions must be drawn: (1) That the introduced California shells vary less in their new environment than they did in the place they came from or (2) that the Staten Island shells have increased remarkably in their variability since 1871, or (3) that place-modes in which time element is not known are of little value in working with organisms of this kind.

9. *Shells of Successive Years Compared.*—Further-

more, the analysis of the 1899 shells indicates that a proper comparison of place-modes of variability could be made only on material of the same relative age, which presumably could be approximated best by collecting the shells in neighboring localities at the same time or in any one locality at the same time in successive years. Consequently lots of 1,000 shells from each of the four Woods Hole localities mentioned in Table V were collected during the first week of August, with some omissions, for several years. These data are assembled in Tables IX and X.

In Table IX it is made apparent that, when the time element is reduced to a minimum by comparing only August 5 shells of various years, the shells of Buzzard's Bay (West Shore and Penzance Point) fall into a group distinct from those of Vineyard Sound (Nobska Point and Barnacle Beach), at least so far as the A. M. is concerned. The A. M. of 11,476 Buzzard's Bay—August 5 shells is 61.330 while the A. M. for 14,503 Vineyard Sound—August 5 shells, is 64.303. In no individual lot of Buzzard's Bay shells does the A. M. reach as high as the Vineyard Sound average and in no one lot of the Vineyard Sound shells does the A. M. fall as low as the Buzzard's Bay average of 61.330.

The standard deviation of the August shells shows no decided grouping with reference to Buzzard's Bay and Vineyard Sound, although those from the latter locality show a slightly higher total average which is probably quite without significance. In general, then, it may be said that during the first week of August the Buzzard's Bay shells show a lower ratio of greatest shell-aperture to height (and consequently may be regarded as rather more advanced in their life cycle) than those of Vineyard Sound, but that they present no significant difference in variability.

In each of the two general localities which were more exposed to the open water and the beat of the waves, viz., Nobska Point and Penzance Point, is the variabil-

TABLE IX

A COMPARISON OF AUGUST SHELLS OF VARIOUS YEARS TO SHOW PLACE-VARIATION.

Place.		Time.	Number.	A. M.	σ	P. E.
Buzzard's Bay	West Shore	1898	1,001	58.928	2.339	±.0352
		1899	920	60.308	2.057	±.0323
		1900	405	60.711	2.042	±.0484
		1901	—	—	—	—
		1902	1,000	63.251	3.280	±.0491
		1903	1,000	61.419	2.234	±.0336
		1904	—	—	—	—
		1905	1,000	61.086	2.012	±.0303
		1906	—	—	—	—
		1907	—	—	—	—
		1908	1,000	60.380	2.469	±.0372
	Total		6,326	60.890	2.663	±.0160
	Penzance Point	1898	1,002	61.718	2.737	±.0412
		1899	1,000	60.170	1.982	±.0299
		1900	1,001	60.617	2.008	±.0316
		1901	—	—	—	—
		1902	1,000	64.155	2.938	±.0443
		1903	1,000	62.773	2.086	±.0314
		1904	—	—	—	—
		1905	1,000	61.381	1.970	±.0775
		1906	—	—	—	—
		1907		Too scarce	to collect	
		1908	—	—	—	—
	Total		5,150	61.870	2.814	±.0187
Total for Buzzard's Bay			11.476	61.330	2.805	±.0125
Vineyard Sound	Nobska Point	1898	2,498	62.751	3.041	±.0290
		1899	1,005	64.022	2.312	±.0347
		1900	1,000	66.396	2.449	±.0369
		1901	—	—	—	—
		1902	1,000	66.775	2.707	±.0407
		1903	1,000	64.605	2.128	±.0321
		1904	—	—	—	—
		1905	1,000	63.765	2.653	±.0400
		1906	—	—	—	—
		1907	—	—	—	—
		1908	1,000	63.296	2.719	±.0410
	Total		8,503	64.205	3.048	±.0158
	Barnacle Beach	1898	998	63.942	2.604	±.0393
		1899	1,000	63.281	2.186	±.0329
		1900	1,000	66.798	2.052	±.0309
		1901	—	—	—	—
		1902	1,002	66.085	2.351	±.0354
		1903	1,000	63.526	2.546	±.0383
		1904	—	—	—	—
		1905		Too scarce	to collect	
		1906	—	—	—	—
		1907	—	—	—	—
		1908	1,000	63.017	2.300	±.0347
	Total		6,000	64.442	2.602	±.0160
Total for Vineyard Sound			14,503	64.303	2.865	±.0113

ity (standard deviation) greater than at West Shore and Barnacle Beach, respectively, which were somewhat more sheltered situations.

Turning to Table X, where the August shells are grouped by years rather than by localities, the A. M. is seen to fluctuate with considerable regularity, reaching in 1902 the highest average ratio. It seems not improb-

TABLE X

August Shells Grouped to Show Yearly Variation.

Year.	Locality.	No.	A. M.	σ	P. E.
1898	West Shore	1,001	58.928	2.339	±.0352
	Penzance Point	1,002	61.718	2.737	±.0412
	Nobska Point	2,498	62.751	3.041	±.0290
	Barnacle Beach	998	63.942	2.604	±.0393
	Average	(5,499)	61.899	3.389	±.0218
1899	West Shore	920	60.308	2.057	±.0323
	Penzance Point	1,000	61.170	1.982	±.0299
	Nobska Point	1,005	64.022	2.312	±.0347
	Barnacle Beach	1,000	63.281	2.186	±.0329
	Average	(3,925)	61.981	2.649	±.0202
1900	West Shore	405	60.711	2.042	±.0484
	Penzance Point	1,001	60.617	2.098	±.0316
	Nobska Point	1,000	66.396	2.449	±.0369
	Barnacle Beach	1,000	66.798	2.052	±.0309
	Average	(3,406)	64.139	3.459	±.0281
1902	West Shore	1,000	63.251	3.280	±.0491
	Penzance Point	1,000	64.155	2.938	±.0443
	Nobska Point	1,000	66.775	2.707	±.0407
	Barnacle Beach	1,002	66.085	2.351	±.0354
	Average	(4,002)	65.067	3.012	±.0227
1903	West Shore	1,000	61.419	2.234	±.0336
	Penzance Point	1,000	62.773	2.084	±.0314
	Nobska Point	1,000	64.615	2.128	±.0321
	Barnacle Beach	1,000	63.526	2.546	±.0383
	Average	(4,000)	63.083	2.542	±.0291
1905	West Shore	1,000	61.086	2.012	±.0303
	Penzance Point	149	61.381	1.970	±.0775
	Nobska Point	1,000	63.765	2.653	±.0400
	Barnacle Beach	—	—	—	—
	Average	(2,147)	62.077	2.718	±.0280
1908	West Shore	1,000	60.380	2.469	±.0372
	Penzance Point	—	—	—	—
	Nobska Point	1,000	63.296	2.719	±.0410
	Barnacle Beach	1,000	63.017	2.300	±.0347
	Average	(3,000)	62.321	2.802	±.0244

able that the missing year 1901 would have furnished a higher maximum than 1902, and that in some future year the high average of 1902 may again be attained.

10. *Dense and Sparse Population Compared.*—Two lots of shells collected in 1899 deserve a separate paragraph. They represent the extremes among all the lots collected with respect to the density of the population. They came from localities on the eastern shore of Buzzard's Bay about five miles apart and were collected during the same week.

TABLE XI

	No.	A. M.	σ	P. E.
Quisset-to-West-Shore	862	60.464	3.127	±.0507
West Falmouth	1,000	59.091	1.913	±.0297

The Quisset-to-West-Shore lot was gathered over an area extending fully a mile along the rocky shore and they were so scarce that it was necessary to utilize the low-tide period of two successive days in order to obtain them, and even then only 862 were obtained instead of the usual 1,000. The West Falmouth lot, on the contrary, were all taken within a few minutes from a single rock about five feet in diameter without by any means exhausting the supply.

It may be that the latter, as would be inferred by their proximity, were more closely related to each other than were the former, and consequently they might be expected to present less variation, or it is possible that the Quisset-to-West Shore lot—representing the pioneers or survivors in an apparently inhospitable area—succeeded in maintaining themselves because of their greater variability (*i. e.,* adaptability). Certain it is, at any rate, that they represent the greatest variability (standard deviation) of any lot of shells obtained from the Atlantic coast except a thousand from West Shore in August, 1902, and those already mentioned from Staten Island.

11. *Variation of the Species Urosalpinx as a Whole.*—By combining the data of all the shells measured—a

total of 50,424—it is possible to approximate a measure of the variability of *Urosalpinx as a species* much more nearly than is possible with smaller lots of 1,000. Such a combination is shown in Table XII, which will be seen to furnish the figures for a curve of considerable regularity in which the arithmetical mean is 61.662 and the standard deviation is 3.367±.0071. This standard deviation is exceeded in but a single instance among the smaller lots which make it up—namely, in the 1,664 shells from Staten Island which show a standard deviation of 3.508±.0412.

TABLE XII

Per Cent.	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76
No.	4	15	32	120	289	675	1,510	2,450	3,812	5,052	5,491	5,861	5,515	5,115	4,225	3,647	2,357	1,714	1,161	737	373	181	54	21	8	4	1

A. M., 61.662. σ, 3.367. P. E., ± .007. Total No., 50,424.

12. *Summary.*—1. When two lots of 1,000 *Urosalpinx* shells each are taken from the same locality they resemble each other sufficiently to indicate a character typical for the locality.

2. Lots of shells from different localities vary widely enough from each other to be easily distinguished, indicating thereby that the varying environment associated with different localities exerts a measurable effect.

3. Endemic Atlantic shells (with one exception noted below) vary less than shells introduced into a new environment (California).

4. The shells of Buzzard's Bay have a lower ratio of greater shell-aperture to shell-height than those of Vineyard Sound.

5. When shells from the same localities in successive fortnights are compared there is an increase in the ratio of greater shell-aperture to shell-height (A. M.) and also a slight increase in variability as shown by the standard deviation, except in the case of the shells from Penzance Point.

6. When growth which we detect by taking into consideration the *time*-factor is compared with the environmental factors that depend upon *place,* the former apparently plays the greater rôle in causing variations.

7. As *Urosalpinx* grows larger (older) the ratio of its greatest shell-aperture to its height diminishes with regularity and its standard deviation tends to become somewhat less.

8. Shells from Staten Island whence the introduced California shells were originally derived show greater variability than the California shells.

9. When the August shells of successive years from the same localities are compared the A. M. of the ratio between the greater shell-aperture and shell-height fluctuates with noticeable regularity, reaching a maximum in 1902.

10. Shells from the localities more exposed to the beat of the waves show greater variability than those from the more protected places.

11. When dense and sparse populations are compared the dense population shows less variability.

12. The average mean of the ratio of greater shell-aperture to height of shell for 50,424 *Urosalpinx* shells is 61.662. The standard deviation is 3.367±.0071.

13. *Conclusion.*—So far as the statistical method is able to reveal, it is extremely doubtful whether or not *Urosalpinx* when introduced into a new habitat exhibits greater variability than when in its native habitat. The change in the variability appearing in successive fortnights in shells from the same locality as well as in change showing itself in the August shells from the same locality in successive years is marked enough to indicate plainly the working of an ontogenetic variability independent of environmental modification, that is, a *time*-factor as distinguished from a *place*-factor. In consequence of this it is practically impossible to collect homologous lots of individuals of these shells upon which the place- (or environmental-) factor may be accurately determined.

NUCLEAR PHENOMENA OF SEXUAL REPRODUCTION IN GYMNOSPERMS[1]

CHARLES J. CHAMBERLAIN

University of Chicago

To the cytologist the most interesting phases of a plant's life history are fertilization and the reduction of chromosomes, processes which initiate the sporophyte and gametophyte generations and which are of the utmost importance in any cytological theories of heredity.

We shall not attempt to define fertilization, but shall simply state that, in our opinion, the process is essentially uniform from its first appearance in the fusion of equal gametes in the lower algæ, up to the heterogamy of the angiosperms and, in our opinion, this fusion of gametes, whether they be the equal gametes of the lower algæ or the unequal gametes of the higher plants, always initiates a sporophytic phase in the life history, a phase which normally continues until the reduction of chromosomes brings it to a close and initiates the gametophytic phase.

The gymnosperms have as yet only a single well-established case of apogamy and not even a single case of apospory, and, consequently, their only mode of reproduction, aside from occasional budding, is that resulting from fertilization.

Since the significance of fertilization becomes more intelligible with increasing knowledge of the participating gametes, it is of prime importance to know the structure, evolution and behavior of the sperms and eggs.

Spermatogenesis

The sperms of fossil gymnosperms are almost unknown, but it is safe to say that Cycadofilicales and

---

[1] A paper read by invitation before the Botanical Society of America, Boston, December 30, 1909.

Cordaitales had swimming sperms, and further, that they had no pollen tubes, the pollen grains reaching the female gametophyte directly, then discharging their sperms about as in the living heterosporous Pteridophytes.

Definite knowledge of the structure of the sperm begins with the cycads, where the sperms are so large that they are easily visible to the naked eye. Broadly speaking, their development is like that of most pteridophytes. In the most thoroughly investigated fern, after the spermatogenous divisions have ceased, two blepharoplasts appear in each cell, which then divides so that each of the two resulting cells contains one nucleus and one blepharoplast. From the blepharoplast there is developed a more or less spiral band which gives rise to numerous cilia.

In gymnosperms, with the exception of *Microcycas, Cupressus* and occasionally, *Ceratozamia,* no spermatogenous divisions precede the formation of the cell which is to produce the pair of sperms, and in these three genera it is not known whether the blepharoplast appears any earlier than in the pteridophytes. I suspect that it does not, but it is certain that in the cycads and in *Ginkgo* two blepharoplasts always appear in the body cell which is to produce the pair of sperms, and while the blepharoplasts are at first very inconspicuous, they finally become larger than the nuclei of most angiosperms.

The mature sperm of the cycad consists of a very large nucleus surrounded by a thin layer of cytoplasm in which is imbedded the spiral band with its thousands of cilia. Compared with the sperms of the pteridophytes, the sperms of the cycads are immensely larger and much less numerous. It must be a fact of some significance that the living gymnosperms, with two or three exceptions, have only two sperms, for the production of sperms in pairs is universal from the liverworts to the orchids. Whether the production of sperms in pairs is associated with a separation of sexes is not known. Objections to such a suggestion are easily raised, but the question seems worth investigation, especially since little is known of the behavior of the chromatin during the mitosis by which two sperms are produced from the body cell.

Except in the cycads and *Ginkgo,* there are no motile sperms in living gymnosperms, but, in our opinion, the transition is not so abrupt as some writers believe. The definitely organized male cells of such genera as *Sequoia* and *Thuja* look very much like the young sperms of a cycad immediately after the division of the body cell, the principal difference being the absence of the blepharoplast, which is such a conspicuous feature in the development of the sperms of cycads and *Ginkgo.* In regard to the several genera with well-organized male cells, the statement is made that there are no structures which could be interpreted as the vestiges of blepharoplasts, but the figures accompanying the various accounts are not convincing and it seems entirely possible that vestiges may yet be found.

According to all the accounts, either as expressed in the text or to be inferred from the figures, the body cell in Taxeæ, Taxodieæ and Cupresseæ gives rise directly to the male cells, there being no formation of sperms within sperm mother-cells. The accounts may be correct, but it must be remembered that a competent observer described just such a condition in one of the cycads, where it is now known that the sperms are formed within sperm mother-cells from which they are afterwards discharged. Among the Coniferales, the well-organized male cell is found in the Taxaceæ, Taxodieæ and Cupresseæ.

In the rest of the Coniferales, which means the Araucarieæ and Abieteæ, there are no organized male cells, but only male nuclei lying free in the cytoplasm of the body cell, and this cytoplasm not always sharply limited from that of the pollen tube. Accompanying these male nuclei there are often structures which might be interpreted as the vestiges of blepharoplasts. According to some observers, one of the male nuclei is smaller than the other, possibly indicating the future elimination of the smaller nucleus.

That both the male cell of *Thuja* and the male nucleus of *Pinus* are descendants of swimming sperms is not to be doubted. The male cell of *Thuja* has lost its cilia and, perhaps, is no longer formed within a parent cell, while *Pinus* has gone further and no longer organizes a definite male cell. In this respect, the *Pinus* gametophyte is more widely separated from the ancestral form than is the gametophyte of *Thuja.*

In some genera, like *Torreya* and *Taxus,* the reduction has proceeded in another direction, two male cells being retained, but one of them having become much smaller than the other and having ceased to function, indicating its future elimination.

It is interesting to note that in Coniferales, with the exception of the Podocarpeæ, those forms with definitely organized male cells have no prothallial cells in the pollen grains, while those with the free male nuclei have retained more or less of the ancestral prothallium; *e. g., Pinus* has retained the prothallial cells, but no longer organizes a definite male cell, while *Thuja* has retained the definitely organized male cell, but has lost the prothallial cells. And further, those genera which have retained the definitely organized male cell no longer organize a definite ventral canal cell, having lost the wall between the ventral canal nucleus and that of the egg, a step toward the complete elimination of even a ventral canal nucleus. Whether there are any causal relations among these reductions is not obvious, but it is interesting to note the correlation. If all evolutionary lines would only progress at the same pace, or if we could discover causal relations between the lines, it would facilitate the construction of phylogenies.

OOGENESIS

We have seen that in spermatogenesis the gymnosperms show a reduction series from the highly differentiated motile sperms of cycads to the free male nuclei of *Pinus*. Oogenesis does not cover so great a range, for motile eggs are not found above the thallophytes. In its most primitive condition, the archegonium of the gymnosperms is more reduced than any found in pteridophytes, for there is no neck canal cell. An egg with a definite ventral canal cell, as in *Ginkgo* and *Pinus,* is the most primitive condition found in gymnosperms. Beyond this there is the elimination of the wall between the ventral canal nucleus and that of the egg, as in cycads and many conifers, a natural step in the elimination of the ventral canal nucleus, and in *Torreya,* even the nuclear division has probably failed to take place, so that the central cell functions directly as an egg. A still further reduction is found in *Tumboa* where the incomplete septation of the female gametophyte results in a failure to organize a definite egg; and finally, there is a complete suppression of any septation whatever, so that the egg is represented only by a nucleus with as little organization of cytoplasm about it as can be found in any angiosperm. Thus there has been a gradual reduction of the archegonium from a condition almost like that of the pteridophytes to the most extreme condition found in angiosperms.

Some might suggest that such reductions would have their natural termination in the elimination of all sexuality, with apogamy as the goal. In *Gnetum Ule* there seem to be instances of apogamy. In the cases reported as apogamy in *Pinus* there is the possibility of fertilization by the ventral canal nucleus. Personally, I prefer to regard apogamy as a specialized, unnatural phenomenon, and not as a condition toward which plants are moving.

The behavior of the chromatin in the final stages of both spermatogenesis and oogenesis in gymnosperms seems to be unique. At the formation of the ventral canal cell or ventral canal nucleus, the chromosomes are very small. The ventral nucleus or cell soon disintegrates, but the chromosomes of the egg nucleus form a spirem. From this point there is a period of development for which we have no satisfactory account of the chromatin. The coarse reticulum of the egg nucleus is not chromatin, for most of it may remain after chromatin again becomes demonstrable. To say that the chromatin becomes dissolved in the linin or takes the form of coarse granules or nucleoli, which may or may not be chromatin at all, hardly solves the difficulty. That some of the so-called metaplasm has about the same position as the latest recognizable stages of the spirem, seems to be about all that can be said. It is certain that chromatin has not yet been traced from the telophase of the ventral canal cell mitosis to the resting egg nucleus with any such certainty as in the pteridophytes and angiosperms. The organization of the spirem from the dubious contents of this nucleus has not been traced in any satisfactory way. However, it is perfectly certain that a small and beautifully definite spirem finally appears.

FERTILIZATION

To the cytologist, who is likely to attribute extreme importance to chromatin, these reduction series in the formation of eggs and sperms are very important, since the more there is eliminated from the structures taking part in fertilization, the more accurately can we determine what is essential and what only accessory.

Fertilization has been studied more thoroughly in *Pinus* than in any other gymnosperm. Here each archegonium has its own archegonial chamber and the pollen tube entering it necessarily discharges its contents into the one egg, the two male nuclei, together with the stalk and tube nuclei and also more or less cytoplasm and starch all entering the egg. One of the male nuclei comes into contact with the egg nucleus and the nuclear membranes at the point of contact break down, so that the chromatin of the two nuclei becomes surrounded by the membrane of the egg nucleus. A spirem is formed from the chromatin network of each of the sex nuclei and each spirem segments into 12 chromosomes, so that there are twenty-four chromosomes. These do not fuse with one another, but become so mixed that the male and female chromosomes can not be distinguished. Each chromosome then splits and during the completion of the mitosis twenty-four chromosomes go to each pole to form the first two nuclei of the sporophyte generation. Consequently, during this process which we call fertilization, there has been no blending of the chromatin contributed by the two parents. Whether a real blending takes place as the two groups of chromosomes pass from the telophase of the first mitosis into the resting reticula of the daughter nuclei, is still undetermined. Personally, I am inclined to think that there is no blending, either at this early stage or later, but rather, that the chromatin contributions remain distinct throughout the life history. Whether there is, during the synapsis stage of the reduction division, sufficient fusion to impair the identity of the individual chromosomes, still remains to be demonstrated.

Although the chromosomes of the two groups become so mixed that they can not be distinguished, the well-known mechanism of mitosis makes it certain that one half of each chromosome contributed by the two parents will reach each of the two daughter nuclei resulting from the first division of the fertilized egg. The same mechanism of mitosis makes it very probable that this equal representation of the two parents will continue throughout the life history of the plant.

In all the genera which have been studied, more or less cytoplasm enters the egg with the male nucleus. In the cycads the entire sperm enters the egg and the cilia may continue to move after the sperm is within the cytoplasm of the egg, but the nucleus of the sperm soon slips out from the cytoplasmic sheath and advances toward the egg nucleus, leaving most or all of the cytoplasm in the upper part of the egg. In other forms, like *Torreya*, *Juniperus* and *Taxodium* the cytoplasm of the male cell surrounds the fusion nucleus and takes part in the formation of the embryo, but in most genera, no such cytoplasm is visible and the embryo is formed from a rather small portion of the basal region of the egg, quite remote from whatever cytoplasm may have entered the egg with the male nucleus.

On such evidence we could not claim, logically, that cytoplasm does not play an essential part in inheritance, for the egg at its first segmentation contains cytoplasm brought in with the male nucleus, but we believe that the series which we traced in spermatogenesis presages the final elimination of any cytoplasm as a part of the male contribution, and the series could be carried into the angiosperms, where, in some cases, the male contributes only a nucleus without any cytoplasm.

In nearly all the gymnosperms the immediate response to the stimulus of fertilization is a series of nuclear divisions which follow each other in such rapid succession that no cell walls are formed between the nuclei. The divisions are simultaneous, probably because the nuclei are in a common mass of cytoplasm exposed to the same conditions. In the large eggs of the cycads, the free nuclear divisions continue until there may be more than a thousand nuclei, but in forms with smaller eggs, the period of free nuclear division is correspondingly reduced, so that we can select a series of genera which show more than a thousand free nuclei, 256 nuclei, then 32, 16, 8, 4 and finally no free nuclear division at all, the first nuclear division of the fertilized egg being followed by the formation of a wall between the daughter nuclei.

These early stages in the gymnosperm sporophyte are remarkably like the early stages of the gametophyte, which also has a prolonged period of free nuclear division before walls begin to be formed, but the conditions are also very similar. The most striking difference between the sporophyte and gametophyte in these early stages is that during mitosis one shows twice as many chromosomes as the other. Very soon, of course, the two generations become very dissimilar. It is worth recalling, in this connection, that in some algæ, like

Dictyota and *Polysiphonia*, the two generations remain similar throughout the vegetative period, the only distinguishing feature being the number of chromosomes.

In conclusion, we believe that fertilization is a phenomenon of fundamental importance, and that future investigation dealing especially with the differences between the various chromosomes, differences which may be only fortuitous but which may be constant and important, may throw light upon the problems of variation and heredity. That the fusion of gametes always gives rise to a sporophytic generation and necessitates a reduction of chromosomes somewhere in the life history is not so speculative and the claim is readily admitted for plants above the thallophytes. We believe that it holds even for thallophytes.

In the simplest bryophytes, alternation is already too thoroughly established to throw any light upon the origin of the phenomenon, and the same may well be said of algæ like *Dictyota, Cutleria* and *Polysiphonia.* We believe that even where the first division of the zygote or fertilized egg shows the reduction division, as in *Coleochæte*, there is a true alternation of generations, although the sporophyte generation is very short. The test of a sporophyte is not its longevity. The fertilized egg of a lily is the first cell of the sporophyte, whether it ever divides at all. Consequently, we regard the zygospore of *Ulothrix* or *Spirogyra* and the fertilized egg of *Vaucheria* or *Œdogonium* as sporophytic structures, even if the first division of the zygote should be meiotic, as seems probable. From such a simple beginning, we believe that the more complex sporophytes with more conspicuous alternation have been developed. The gymnosperms throw no light upon the origin of alternation, but show suggestive stages in the reduction of the gametophytes. They also afford an admirable field for the study of some aspects of fertilization, but we can hardly claim that all the problems of this complex phenomenon would be solved with greatest certainty by the study of cycads or pines.

NUCLEAR PHENOMENA OF SEXUAL REPRODUCTION IN ANGIOSPERMS[1]

PROFESSOR D. M. MOTTIER

Indiana University

What constitutes sexual reproduction, fertilization or fecundation is so variously set forth in botanical literature that one naturally approaches a discussion of this subject with some timidity. Having been assigned the group angiosperms, in which a definition of sexual phenomena may be made more specific by concrete illustration, it seemed at the outset that a part of my task, at least, was simpler than that of some of my colleagues who take part in this section of our program; but a moment's thought convinced me that what might be gained from this limitation of my field was probably much less than the opportunities offered by the scope and diversity of phenomena in groups of lower plants.

In the preparation of this paper, the writer has kept clearly in mind the fact that the phenomena of sexual reproduction implies explicitly that a special significance is attached to the nucleus as in a large measure distinct from any function, or rôle of the cytoplasm; consequently he will deal first chiefly with nuclear behavior, leaving a discussion of the relation of nucleus and cytoplasm to be dealt with in a later paragraph.

Sexual reproduction in phanerogams implies the union of especially developed cells known as gametes, and the development of an individual plant from such union. While in this process the union of the nuclei is held to be more important, it is not inferred that the part taken by the cytoplasm is unimportant, but the writer does insist that the cytoplasm plays a secondary rôle in the most important results of sexual reproduction, namely, the transmission of parental characters. It will be maintained also that the union of mere gametophytic cells does not constitute fecundation, or a sexual process in phanerogams, nor is parthenogenesis—if such really exists in seed plants—to be confused with apogamy, nor apogamy with the various sorts of vegetative propagation of the sporophyte. Lastly, it is likewise the duty of the student of fecundation to consider the phenomena of graft hybrids which have been reported in recent literature, for such phenomena may have a profound significance in the shaping of future theories of sex and heredity, and on sex determination and control.

---

[1] A paper read by invitation before the Botanical Society of America, Boston, December 30, 1909.

The problem of sexual reproduction in higher plants, and in lower ones as well, is complicated by the existence of two distinct phases, or individuals, in a life cycle, namely, the gametophyte and sporophyte; for it is necessary, in dealing with the rôle of the nucleus in sex, to consider a complete life cycle. Now gametophyte and sporophyte in phanerogams are fundamentally different hereditarily, and this difference is due chiefly to the fact that the former possess the haploid, or x number, of chromosomes, and the latter the diploid, or $2x$ number. Whatever respect or disrespect one may have for the "sacred" x and $2x$ number of chromosomes, the fact of their importance in any theory of sex and heredity remains the same, and must be taken into consideration. It is, of course, quite familiar to all that the change from sporophyte to gametophyte occurs in the formation of the spores, and that this change consists in the reduction of the number of chromosomes from the diploid, $2x$, to the haploid, x number; that this reduction is accomplished during the first mitosis in the spore mother-cells, this division of the nucleus being acknowledged as qualitative or differential. A detailed description of the evolution and behavior of the chromosomes during the tetrad divisions, and a discussion of controversies and of the different views held in regard to this evolution, or in regard to the differential character of any chromosome or set of chromosomes—are features which can not find consideration within the limits of this paper. I wish to state also that in the use of the expression, sexual reproduction, I shall keep in mind primarily, and for the sake of clearness, what will be called a complete sexual angiosperm, hereditarily speaking, that is, one with a complete life-cycle, embracing both sporophyte and gametophyte. Such an individual arises from the fusion of egg and sperm, each with the haploid number of chromosomes. The product of this fusion must develop into an adult sporophyte, capable of producing functional micro- and mega-spores, each with the haploid number of chromosomes. From this it will be seen that the mere fusion of gametophytic cells or nuclei is not necessarily regarded as a sexual process. It is to be understood also that the writer does not consider it imperative to stay within the confines of the foregoing definition, for like nearly all general definitions, this is made for convenience and for greater clearness in the general presentation.

No profounder statement has been made within the past half century than when it was said that the union of two sexual cells created a new individual—the individual with just twice the number of chromosomes as that possessed by either parent cell, namely, a sporophyte; for is it not the sexual process that makes possible all those phenomena understood by the expression, transmission of parental characters to offspring? And I mean especially the transmission of characters of two direct parents to each new generation. In this connection may we not ask also whether hereditary phenomena, such as engage the attention of biologists at the present day, exist among those simple plants in which sexual reproduction does not occur? Is there such a thing as phylogeny in plants that are without sex? The limits of this paper prohibit an attempt at an answer to the last two questions at this time. We shall have in mind then those characteristics which are handed down from parents to offspring. Some of these characters may manifest themselves in the progeny with varying degrees of intensity, or in such combinations that entirely new marks or characters may appear; consequently characters are spoken of as dominant, recessive, latent, etc., and it not infrequently happens that estimates are placed upon absent characters. All of this implies that these external marks of living things are the manifestations of the activities of certain parts of the living substance, which are in competition, or among which there is an unceasing struggle. Attempts are also made to predict, by means of mathematical formulæ—and with surprising success in some cases—which of these forces or activities will gain the upper hand and dominate, and which will be secondary. Furthermore, sexual reproduction in phanerogams always implies a something that we know as maleness and femaleness, and this maleness and femaleness are phenomena which distinctively characterize the gametophytes. Maleness and femaleness may, in certain cases, give a distinctive mark to the sporophyte, as in diœcious plants, if we admit that such a thing as an absolutely diœcious sporophyte exists in angiosperms. But male and female marks are first manifested in the sporophyte of most seed plants by the production of the pollen and of the megaspores, which production is, of course, a matter of heredity. In the formation of pollen, it is well known that it is the nucleus which undergoes the important and complicated changes in division; the cytoplasm, so far as present knowledge extends, is halved arbitrarily. The same is likewise true in the development of the megaspores. In the case of each spore mother-cell, a qualitative division takes place, by which, as experimental evidence seems to indicate, different intensities of maleness and femaleness pass respectively to the several resulting cells. Both male and female gametophytes with their developing gametes grow under similar environmental conditions, namely, that of a parasitic habit within living tissue. The sperms of the pollen tube consist mainly of nuclei, with scarcely any distinctive characteristics in the scanty cytoplasm. These nuclei contain the haploid number of chromosomes. In the development of the egg, the same number of chromosomes is strictly preserved, no matter what mitotic peculiarities may be observed in any other cells of the embryo-sac, apart from the egg-apparatus. The egg differs from the sperm in appearance chiefly in the amount of cytoplasm present, but the cytoplasm of the one is similar to that of the other. Apart from difference in shape, which is of no importance in phanerogams, the sexual nuclei reveal identical chromatin structures at the time of union, for both are in the resting, or non-mitotic state. Chromatin granules of the sperm nucleus mingle with those of the egg. When the nuclear membranes between the two contiguous nuclei have disappeared, it is not possible to distinguish paternal from maternal chromatin. It is not seen that chromatin particles of the sperm fuse or become paired with those of the egg nucleus. The gamete nuclei do not remain in any manner separate or distinguishable from each other, as in certain lower plants and in some animals, and one of the very interesting and important problems from the standpoint of hereditary considerations is the relation of male and female chromatin, during the life of the sporophyte. A number of authors have offered explanations of this relation based on observations made upon the first, or heterotypic, mitosis in the spore mother-cells, *i. e.*, at the end of the sporophytic cycle. Strasburger ('05) and Gregoire ('05), together with a number of their more recent students, maintain that the maternal and paternal homologous chromatin parts become associated in pairs previous to and during the synaptic balling up of the nuclear contents in the first mitosis of the spore mother-cells. This process, they assert, leads to the formation of two spirems (one paternal and one maternal) which become united side by side, to form the double chromatin thread, in which the homologous parental chromatin parts are brought near to each other.

The writer (Mottier, '07, '09) does not agree with this view. From a careful and extended study of mitosis in spore mother-cells of higher plants, he is convinced that, confirming the observations of Farmer ('05) and others, there is no development of maternal and paternal spirems which unite laterally to form the double chromatin thread or spirem in the mitosis under consideration, but that the sporophytic chromosomes are arranged in a lineal series in the heterotypic spirem, and that consequently the two members of each bivalent chromosome are brought side by side, in case such an arrangement is attained by the two members of each bivalent, by a folding, looping or lateral approximation of parts of the spirem. In his own studies the writer is unable to find any justification of the doctrine that maternal and paternal chromatin is represented in definitely recognizable lumps designated by some observers as prochromosomes. While I can not agree with the view advocated by Strasburger and Gregoire, namely, the presynaptic or synaptic union of two spirems (male and female), because of my personal studies, I am also unable to accept their explanation upon the ground of theoretical considerations. Let us return for a moment to the fusion nucleus of the fecundated egg. It is perfectly clear that, soon after nuclear fusion, paternal chromatin elements, let us say, pangens, are indistinguishable from maternal elements. These pangens, assuming always the individuality of the chromosomes and of the pangens, correspond in form, size and staining qualities. The nucleolus or nucleoli of the egg are also similar to those brought in by the sperm, in case nucleoli are demonstrable in the sperm nucleus. There is nothing to lead one to believe that the parental pangens do not mingle in the resting nucleus (*i. e.,* not in mitotic activity). If there is a pairing of homologous parts, or exchange, inter-relation, or "Wechselwirkung" of pangens, or of any hereditary bearers, what reason is there to believe that such should not take place soon after fecundation, rather than at the close of the sporophytic ontogeny, or the beginning of gametophytic development? If the nature and development of the sporophyte, from the standpoint of its inherited characteristics, is determined by what is transmitted to it by its parents, how may these parental tendencies operate unless they are intimately associated—unless some mutual relation, or a "Wechselwirkung" of the entities representing these tendencies, is in continuous activity? Furthermore, when the fusion nucleus of the fertilized egg in angiosperms divides, the spirem separates by cross segmentation into the $2x$ number of chromosomes, x being male and x female. These sporophytic chromosomes are arranged in lineal series, or end to end, to make the spirem, which splits longitudinally. I do not believe many cytologists will contend that the sporophytic spirem is formed by the lateral coming together of male and female spirems. If the parental chromosomes are arranged tandem to form the sporophytic spirem, why should they be arranged in any other manner to form the heterotypic spirem?

Returning now to the fecundated egg, it is seen that the fusion nucleus presents the same visible structure as that of either gamete, with the exception that an additional nucleolus or nucleoli may sometimes be observed. The essential demonstrable act in this fusion concerns the nuclei; the behavior of the cytoplasm that may accompany the sperm nucleus is largely a matter of conjecture, for it is not possible to trace its behavior with any degree of accuracy, either in the living state, or by means of the indirect method of study. However, to satisfy the demands of the most radical we may admit that sperm cytoplasm unites with egg cytoplasm in the act of fecundation. I have described in some detail the structural union of the sexual nuclei; for in a later paragraph will be discussed the relative significance of nucleus and cytoplasm in sexual reproduction, and as factors in the transmission of hereditary characters.

One male nucleus of the pollen-tube is concerned in sexual reproduction as that term is understood in this paper, but as the union of the second male nucleus with the polar nuclei in a number of plants has been associated with, if not actually regarded as, a sexual act, the phenomenon will receive a brief mention. In 1897, the writer (Mottier, '97) called attention for the first time to the fact that the second male nucleus applied itself to one of the polar nuclei in *Lilium Martagon,* and shortly after that date the actual union of this male nucleus with the endosperm nucleus of the embryosac was reported for various plants by different observers. Guignard spoke of this nuclear union as a second fecundation, hence arose the idea of "double fecundation" in phanerogams. The fusion of the two polar nuclei and the second male nucleus resembles physically the real sexual union, as do also nuclear fusions in ordinary vegetative cells wherever such may occur. It recalls a sexual act in subsequent behavior, for it is maintained that endosperm thus arising is of a hybrid character, and that this hybrid character is due to the hereditary influence of the male nucleus. The hereditary influence of the second male nucleus upon the endosperm we may admit for the sake of argument, for whatever else this phenomenon may signify, it certainly shows the greater importance of the nucleus in the transmission of characters. But, that this union of nuclei in the endosperm cell is not a sexual process, as defined in a foregoing paragraph, is seen in the fact that the endosperm is merely a continuation of the female gametophyte, developed subsequent to fertilization of the egg, and for the nourishment of the sporophyte, just as a fern prothallium may continue its development, following the fecundation of an egg and its subsequent development into the embryo fern.

In a group of organisms in which a structure or function is so universally present, the absence of the same in any one or several of such organisms elicits at once our attention, and, in this respect, apogamy and parthenogenesis become of special interest. Although apogamy and parthenogenesis do not involve the sexual act, yet an accurate and intimate knowledge of these phenomena is likely to modify profoundly our views of sexual reproduction, especially if a series of generations of apogamously produced plants be compared with a series of sexually produced individuals, of the same or related species, in regard to the subject of variation, individual vigor, manner of propagation, transmission of certain characters, etc. The term apogamy is here used to signify the development into an embryo of the egg-cell possessing the double or $2x$ number of chromosomes without the union with a sperm nucleus from the pollen-tube (somatic parthenogenesis of Winkler, parthenopogamy of Farmer and Digby). It is not deemed desirable to connect the word parthenogenesis with such a process, for a reproductive cell, although developed morphologically as a gamete, is not so considered unless it contain the reduced number of chromosomes. Accordingly, the term parthenogenesis will be applied only to the development into an embryo sporophyte of an egg containing the x number of chromosomes.

In recent years several notable cases of apogamy among phanerogams have been described, among which may be mentioned *Antennaria alpina* by Juel (1900), species of *Alchimilla,* especially of the group Eualchimilla by Murbeck and Strasburger ('04), *Taraxacum officinale* by Juel, *Wikstroemia,* by Winkler, together with several others from different families of plants. In *Antennaria alpina,* for example, the tetrad divisions do not take place in the megaspore mother-cell which functions at once as the megaspore. Naturally this cell contains the diploid number of chromosomes. From this cell there develops an apparently normal embryo sac, with the exception that the polar nuclei do not unite. The cell which represents the egg develops without fecundation into an embryo sporophyte. The process in the other species mentioned is in the main similar to that of *Antennaria alpina,* differing only in certain details, which may not be enumerated here. While, in these apogomous species, an apparently normal gametophyte develops, it may be very seriously questioned whether such embryosacs, whose egg-cells contain the these apogamous species, an apparently normal gametophytic. However, progress in science is not accomplished by controversies and discussions of terminology. The main thing which interests us here is the effect, from an hereditary standpoint, that apogamy, of the sort mentioned, has upon the species so affected. True it is that such apogamous progeny have the characters of both parents, male and female, but it is a remote parentage. There is no new parent introduced with each new generation, that is, each time a plant comes from a seed, and it seems not improbable that the loss of certain very important reproductive functions may be expected in later generations of such plants. In reality certain observed facts seem to bear out this suggestion, as Strasburger found that, in some of the Eualchimillas, degeneration took place in the pollen mother-cells before the spores were fully formed. Whether apogamously developed plants will behave in a manner similar to those propagated vegetatively, *e. g.,* by cuttings, or as normal sexually produced individuals, future research must determine. Until the observations of the several observers have been confirmed by others, and until experimental cultural studies are made to ascertain the behavior of apogamous plants along with those possessing sexuality, speculation seems idle.

In regard to parthenogenesis as defined in a preceding paragraph, this phenomenon is claimed to occur in certain species among rather widely separated families. The best known instances are *Thalictrum Fendleri*, as reported by Day (1896), *Thalictrum purpurescens,* by Overton (1902, 1904) and *Wikstrœmia indica*, by Winkler (1904, 1905). However, for *Thalictrum purpurescens,* Overton (1904, p. 278) expressly states that in some cases no reduction in the number of chromosomes occurs in the embryosac mother-cells, and that tetrads are not formed, so that apogamy certainly occurs in this species also. In regard to *Wikstrœmia* it may be added that the recent investigations of Strasburger upon this plant and other Thymelaceæ, point rather towards apogamy than parthenogenesis.

Even more perplexing to the student of sex and heredity than apogamy or parthenogenesis are the phenomena presented by what are known as graft hybrids. A number of seed plants of a hybrid nature are known to botanical science, which have not arisen by means of seed production, but presumably from the callus formed at the juncture of the stock and scion in grafting. The most noted of these is, of course, *Cytisus Adami,* which is supposed to have arisen from *Cytisus laburnum* and *Cytisus purpureus* as a graft hybrid. This problem, which has held, in a large measure, the interest of biologists for about eighty years, seems now to be on a fair way towards a solution, having as a starting point the production of a graft hybrid experimentally. Hans Winkler, as is well known, has produced a plant which, in point of flower, fruit and foliage, seems to be a hybrid between the common nightshade *Solanum nigrum* L. and the tomato, *Solanum lycopersicum* L. of the King Humbert yellow-fruited variety, by an ingenious method of grafting in which the nightshade was used as the stock and the tomato as the scion. Perhaps a very brief statement of the process may not be out of place here.

Using the cleft method of union, Winkler grafted vigorous shoots of the seedling tomato upon the stem of the nightshade. As soon as union had taken place the scion was cut off near its base in such a way that the apical cut surface consisted partly of nightshade and of tomato tissue. Of the adventive shoots arising only those which sprang from along the line of union of the two specifically different tissues were allowed to grow. In one particular case fourteen of such sprouts were removed and transplanted as cuttings. Of these eight proved to be *Solanum nigrum,* five pure *Solanum lycopersicum,* and one the hybrid in question. This plant grew to flower and fruition, and as stated in the foregoing, revealed hybrid characters in stem, leaf, flower and fruit. This hybrid Winkler named *Solanum* *tubingense* H. Wklr. (*S. nigrum* L. + *S. lycopersicum* L., 1908). For a detailed description of the plant the reader is referred to the original publication.[1] That the conditions under which such a graft hybrid is produced are very rarely fulfilled, is seen in the fact that from the 268 graftings made by Winkler in 1908, 3,000 adventitious shoots were developed after decapitating the graft in the manner described, and of these 3,000 the vast majority were specifically pure; five were chimeras, and one the hybrid referred to. Now the all-absorbing question for the cytologist is: By what means are parental characters transmitted in cases of this sort? Of course speculation is futile until the histological facts are known, but, assuming that such shoots are real hybrids, two guesses may be offered. There may have been (1) a migration of nuclei from cell to cell and their subsequent fusion, as in certain fern prothallia developing apogamous sporophytes, or (2) the hereditary transmission may have been accomplished by cytoplasmic union between cells, or by some sort of enzyme action.

It is highly probable that these remarkable adventitious shoots are not true hybrids, but mere chimeras.

In a personal communication, Dr. Winkler has very kindly informed me that seeds of "*Solanum tubingense*" produced pure nightshades (*Solanum nigrum*), and those of "*Solanum proteus*" pure tomatoes (*Solanum lycopersicum*).

The fact that seeds of "*Solanum tubingense*" produced pure nightshades seems to be conclusive evidence that the structure in question is not a hybrid, but merely a remarkable chimera. Strasburger ('09) has just published the results of a histological study of the tissues formed at the juncture of stock and scion in grafts of *Solanum nigrum* and *Solanum lycopersicum,* and he reports that neither nuclear migrations from one vegetative cell to the other nor nuclear fusions in any of these cells were observed. These results are in accord with the same author's cytological studies on other supposed graft-hybrids. Winkler's histological studies on "*Solanum tubingense*" have not yet been made public, but all the facts thus far seem to indicate that so-called graft-hybrids, including *Laburnum Adami,* the *Bizzarrias* and those of *Mespilus,* etc., are only vegetable chimeras.

---

[1] *Ber. d. Deutsch. Bot. Gesellsch.*, 26*a*: 595–608, 1908.

At the juncture of stock and scion in grafts, especially in the case of those that produce adventitious shoots of such remarkable character, there is a cell-complex formed of the vegetative cells of two specific individuals, and the specifically different cells may be regarded as being so intermingled and reacting upon each other in such a manner as to produce adventitious shoots of an almost exact hybrid character in so far as vegetative marks are concerned. In the case of Winkler's "*Solanum tubingense,*" whose seeds gave only pure nightshades, it is clear that both egg and pollen were descended from pure nightshade cells, as the nightshade and the tomato do not cross.

Although the problem of the so-called graft hybrids can not be regarded as definitely settled, yet nearly all the facts go to strengthen the view that hybrids are formed only by the union of cells and nuclei sexually differentiated, and that fecundation and the transmission of characters are not accomplished by the protoplasm in general, nor by the action of an enzyme, nor is it the expression of metabolism, but by the *union of specific material entities in the sexual nuclei.*

Although the concensus of opinion among biologists attributes to the nucleus by far the most important rôle in the process of sexual reproduction in its fullest significance, yet there is still some difference of opinion in regard to the relative functions of nucleus and cytoplasm in imparting the stimulus to growth and cell division, and in the transmission of parental characters—the two chief constellations of phenomena following the sexual act.

To arrive at any satisfactory conclusion in the light of existing literature, a careful analysis of cell structure and of the functions more directly concerned is necessary, both from the standpoint of phylogeny and from that of the individual, or individuals concerned. Careful investigations of recent years upon the cells of certain lower plants seem to justify the opinion that the more original or primary protoplasm is to be conceived as being entirely without organized nuclei, possessing uniformly in all parts its formative and nutritive functions. Then there gradually came about, phylogenetically speaking, a separation of the constructive, nutritive—and may we also say—directive functions in this substratum, those parts of the plasm having formative activities being the first differentiated bearers of hereditary characteristics. These particles or granules may have remained for a long time distributed in the general plasmic mass, just as we find in certain existing Cyanophyceæ and bacteria "chromatin bodies" distributed throughout the cell rather than collected in a typical nucleus. The next step in the evolution of more differentiated protoplasm occurred when the formative parts, be they known as chromatin bodies, or what not, became separated from the surrounding plasm by a membrane, or, in other words, the creation of nucleus as distinct from cytoplasm. In the light of known facts no one, I think, will seriously believe that among the lower plants the nucleus is as highly differentiated as among seed plants, consequently a larger number of functions must have been performed by the various hereditary units, and a much simpler method of nuclear division demanded. This view seems well borne out by the simpler method of nuclear division in certain lower plants and in cells of higher plants, which have taken on a purely vegetative rôle, and which divide by the direct method or fragmentation. As soon, however, as differentiation in the hereditary units increased, a much greater complexity in the mechanism of division followed, a conclusion to which the mitotic phenomena in higher plants stand as incontestible testimony. On the other hand, we do not mean to imply that progressive differentiation was confined to the nucleus alone, for the cytoplasm of higher plants reveals evidence of unmistakable differentiation. I do not allude to the alleged hereditary substance, chondrosomes, to be mentioned beyond, but merely to such differentiation as spindle fibers, which in many higher plants are almost wholly of cytoplasmic origin. As is well known, Strasburger has endeavored to make things clearer by applying to such parts of the cytoplasm as spindle fibers centrosomes, centrospheres and the plasma membrane of the cell, the term kinoplasm, attributing to this substance certain activities. The researches of Noll upon marine algæ indicate with a very high degree of probability that the plasma membrane is the part of the protoplasm which takes a leading part in responding to external stimuli. The doctrine that an enucleated cell can not do any constructive work, as, for example, forming a cellulose wall, has become so generally accepted that the same has found its way into general reference works. This doctrine has in recent years been disputed, but so far as I am aware it has not been satisfactorily disproved. I shall not bring into this category such cytoplasmic differentiations as chloroplasts and other plastids, but enough has been said to indicate that the cytoplasm as well as the nucleus is a differentiated body, which means a diversity of functions or activities. Now, although cytoplasm and nucleus have certain functions that seem in a large measure independent, yet the interrelation of these two parts of the cell is such that neither can exist and function to any great extent without the other. No one has up to the present time been able to isolate a nucleus and keep it alive any length of time apart from living cytoplasm. Whatever the nucleus does, it must do in connection with living cytoplasm. The cytoplasm is in a sense the special environment of the nucleus, and it is in this environment that the nucleus must exist and function. It is also reasonable to believe that, in certain functions of the nucleus, the cytoplasm acts largely as an environmental factor. It is, however, an environment so intimately connected with the nucleus that even a momentary separation may prove fatal, for the skill of the experimenter in this field is yet to be demonstrated.

On the other hand, while the cytoplasm may exist for some time wholly apart from a nucleus, and although during this separate existence the cytoplasm may respond to certain stimuli, yet it can not do constructive work—a phenomenon which seems to indicate roughly the chief province of these two parts of the living cell.

In the light of the foregoing analysis, we may now consider some results obtained by indirect methods, and through certain experiments.

Since the declaration of O. Hertwig in 1875, that fecundation consisted essentially in the union of an egg and a sperm nucleus, this doctrine has received general acceptance. Some observers maintain that this idea places undue emphasis upon the importance of the nucleus, and claim that the cytoplasm is almost of equal significance. In a recent publication Meves ('08) describes in great detail rod or thread-like bodies in the cells of the very young embryo of the chick, which he designates as chondriosomes, and which he regards as cytoplasmic bearers of hereditary characters. The same author in 1904 described and figured similar rods and threads as occurring abundantly in the tapetal cells of *Nymphæa alba*. In the tapetal cells of the anther of *Ribes Gordonianum*, Tischler ('06, p. 573) calls attention to slender rods of varying length, which he designates as chromidial substance, stating that they came out of the nucleus. The writer has examined many thousands of tapetal cells from various plants, fixed and stained in a manner quite similar to that used by Meves, but no such bodies have been found as those figured by this author. It is not my intention to discuss this phase of the subject from the standpoint of zoological literature, but it may be said that tapetal tissue is not the place that a botanist would go to look for especially differentiated hereditary substance. If hereditary substance, such as Meves attributes to the cytoplasm of tapetal cells, really exists, it seems very strange to a plant cytologist that it can not be demonstrated in spore mother-cells, where, above all parts of the plant, protoplasmic structures are most clearly brought out.

As stated in the foregoing, fecundation manifests two constellations of phenomena, the transmission of parental characters and the power of growth and division of the egg. That these two categories are in a measure distinct is amply attested by phenomena of common observation, and by experimental evidence. That various sorts of environmental stimuli, from the sting of an insect to the increased osmotic power of surrounding water, will impart to living cells the power of growth and division is well known. The sting of an insect, for example, will stimulate growth and cell division in stem and leaf, which results in a gall; the presence of a pollen tube will induce an ovule to grow to mature size though no embryo develops within it. In these and in other similar cases, too numerous to mention, we have merely responses to external stimuli, for doubtless the pollen tube may act as an external stimulus, and no one will contend that these phenomena have to do with the transmission of parental characters. From our standpoint the phenomenon of artificial parthenogenesis merits especial attention. When the egg-cells of certain marine animals are stimulated to develop by external agencies of whatever sort, it has become fashionable to speak of the fact as fertilization, but whatever meaning be put into the word fertilization, the phenomenon in question is not fecundation or sexual reproduction. Even though in every case the most sanguine expectations of the experimenter be realized, namely, the development into an adult of an egg thus stimulated, the process would teach us nothing more about sexual reproduction and the transmission of parental characters than ordinary parthenogenesis. The fact that a larva having purely maternal characters will develop from a sea-urchin egg with which the sperm of a starfish had united, does not show that hereditary characters are handed down by the cytoplasm. If, on the contrary, the gastrula, showing only maternal characters, which Godlewski ('06) reared from the union of an enucleated egg-fragment of the sea-urchin and the sperm of a crinoid, could have developed into an adult, or even into the larval stage, which still revealed only maternal characters, the cytoplasm might have regained some of its old-time prestige, but even then it is doubtful whether that fact would have wrested from the nucleus its monopoly as a transmitter of parental characters.

In such cases as the embryo hybrid of sea-urchin and starfish, mentioned in the foregoing paragraph, it seems very probable indeed that the cytoplasm of the egg directs and even controls the growth of the embryo for a short time subsequent to fecundation, but it is very improbable that the cytoplasm does more. Even in the case of a complete fusion of the egg and sperm nuclei, this and similar experiments seem to indicate only the dominance of the egg nucleus over that of the strange sperm. With the egg nucleus operating in its own special environment, and attributing a directive or regulative function to the cytoplasm, the result is what might reasonably be expected. That the cytoplasm is differentiated, and that it directs or regulates the formation of certain parts of the embryo in some animals, is clearly shown by the various interesting and important studies of cell lineage carried out by Conklin ('05) and others. Important and far-reaching as are these studies in contributing to our knowledge of living protoplasm, they do not teach us very much concerning the cytoplasm as an heredity bearer, nor do I understand that the respective observers make such claims.

The stimulation of egg-cells to growth and division by immersing them in water having different physical or chemical properties than their normal surroundings, or by injecting chemicals into the ovaries or ovules by means of an hypodermic syringe, are lines of study that are valuable and interesting in showing the response of living cells and tissues to external stimuli, for it is the business of the physiologist to know what cells can do under any and all conditions; but that these experiments have anything to do with sexual reproduction or in elucidating the more fundamental principles in the evolution of organisms connected with sexual reproduction, still remains to be seen.

On the other hand, if one regards the elementary life processes merely as the expression of metabolism, then hereditary peculiarities are only the expression of metabolism. That which is inherited is for each organism only that kind of metabolism peculiar to the organism. Of course, the writer can not subscribe to this view. Neither does he maintain that the cytoplasm takes no important part in sexual reproduction. He has called attention to the opinion that the stimulus to growth and cell division which follows every sexual act fully accomplished, and which may be brought about apart from the act of fecundation, has been confused with the main result of sexual reproduction, namely, the transmission of parental characters. It is held that the present state of our knowledge still maintains the doctrine that the "monopoly" of transmitting hereditary characters still belongs to the nucleus, and that these hereditary parental characters are represented in the nucleus by material entities. It matters little whether we speak of these material representatives as pangens, or what not. The opinion is expressed that the chief function of the cytoplasm, apart from purely nutritive activities, in its relation to the nucleus is directive or regulative in the sense of being responsive to external stimuli. In so far as the transmission of parental characters go, the cytoplasm plays about the same rôle compared with the nucleus as the environment does in the development of the individual organism.

PAPERS CITED.

Conklin, E. G., '05. Organ-forming substances in the eggs of Ascidians. *Biol. Bull.*, 8: 205–230, 1905.

Farmer, J. B., '05. On the maiotic phase (reduction division) in animals and plants. *Quart. Jrnl. Mic. Sci.*, 48: 489–556, 1905.

Godlewski jun., Emil, '06. Untersuchungen über die Bastardierung der Echiniden- und Crinoidenfamilie. *Archiv f. Entw.-Mech.*, 20: 578–642, 1906.

Gregoire, V., '05. Les cinèse de maturation dans les deux règnes, etc. *La Cellule*, 22: 221–376, 1905.

Guignard, L., '99. Sur les anthérozoides et la double copulation sexuelle chez les végétaux angiosperms. *Revue Gen. de Bot.*, 11: 129, 1899.

Juel, H. O., '00. Vergleichende Untersuchungen über typische und parthenogenetische Fortpflanzung bei *Antennaria, Kongl. Sv. Vet. Akad. Handlingar*, 33: 1–59, 1900.

—— '05. Die Tetradenteilungen bei Taraxacum und anderen Cichorieen. *Kungl. Sv. Vet. Akad. Handlingar*, 39: 1–20, 1905.

Meves, Fr., '04. Ueber das Vorkommen von Mitochondrien bezw. Chondromiten in Pflanzenzellen. *Ber. d. Deutsch. Bot. Gesellsch.*, 22: 284, 1904.

—— '08. Die Chondriosomen als Träger erblicher Anlagen. Cytologischen Studien am Hühnerembryo. *Arch. f. Entw.-Mech.*, 72: 816–865, 1908.

Mottier, D. M., '97. Ueber das Verhalten der Kerne bei der Entwicklung des Embryosacs, etc. *Jahrb. f. wiss. Bot.*, 31: 125–158, 1898.

—— '07. The development of the heterotype chromosomes in pollen mother-cells. *Ann. Bot.*, 21: 309–347, 1907.

—— '09. On the prophases of the heterotype mitosis in the embryo-sac mother-cell of *Lilium*. *Ann. Bot.*, 23: 343–352, 1909.

Overton, J. B., '02. Parthenogenesis in *Thalictrum purpurescens*. *Bot. Gaz.*, 33: 363–375, 1902.

—— '04. Ueber Parthenogenesis bei *Thalictrum purpurescens*. *Ber. d. Deutsch. Bot. Gesellsch.*, 22: 274–283.

Strasburger, E., '05. Typische und allotypische Kernteilung. *Jahrb. f. wiss. Bot.*, 42: 1–70, 1905.

—— '04. Die Apogamie der Eualchimillen und allgemeine Gesichtspunkt, die sich aus ihr ergeben. *Jahrb. f. wiss. Bot.*, 41: 88–164, 1904.

—— '07. Ueber die Individualität der Chromosomen und die Propfhybriden-Frage. *Jahrb. f. wiss. Bot.*, 44: 482–555, 1907.

—— '09. Meine Stellungnahme zur Frage der Propfbastarde. *Ber. d. Deutsch. Bot. Gesellsch.*, 27: 511–528, 1909.

Tischler, G., '06. Ueber die Entwicklung des Pollens und der Tapetenzellen bei *Ribes* Hybriden. *Jahrb. f. wiss. Bot.*, 42: 545–577, 1906.

Winkler, H., '04. Ueber Parthenogenesis bei *Wikstrœmia indica* (L) C. A. Mey. *Ber. d. Deutsch. Bot. Gesellsch.*, 22: 573–580, 1904.

—— '06. Botanische Untersuchungen aus Buitenzorg. II., 7. Ueber Parthenogenesis bei *Wikstrœmia indica* (L) C. A. Mey. *Ann. du jardin botan. de Buitenzorg*, 2 Ser., 5: 208–276, 1906.

—— '07. Ueber Propfbastarde und pflanzliche Chimären. *Ber. d. Deutsch. Bot. Gesellsch.*, 25: 668, 1907.

—— '08. Solanum tubingense, ein echter Propfbastard zwischen Tomate und Nachtschatten. *Ber. d. Deutsch. Bot. Gesellsch.*, 26*a*: 595–608, 1908.

SHORTER ARTICLES AND DISCUSSION

STERILITY[1]

THE problem of sterility presents many points of interest to the biologist, whether he be a clinician, breeder of plants or animals or a pure biologist, both from a descriptive and an experimental aspect. By the physician, the failure of individuals to produce children in marriage is designated by this name, although the causes may be widely at variance in different cases. Thus, the failure may be due to the impotence of the male, induced by a variety of causes, such as congenital impotence, where sex cells are not formed, although the organs themselves may be apparently normal; or evident deformities may occur such as the failure of one or both testes to descend (cryptorchism); again, impotence may be induced by disease, such as gonorrhœa, syphilis and the like; or again, through presenile debility caused by excessive activity of the organs concerned. On the other hand, the failure to produce offspring may be due to the corresponding impotence of the female, or it may result from wholly secondary causes, such as the failure of the ovum to become fixed. All of these cases are grouped, collectively, under the term sterility. Very frequently a simple operation upon the uterus of the female is sufficient to cause the ovum to become fixed, so that subsequent ovulations, accompanied by fertilization, result in offspring and the sterility disappears. With congenital sterility, where no sex cells are formed, the case is obviously different, for the condition there is permanent. Cases of congenital sterility seem to be rare, although it is exceedingly difficult to obtain concise data upon the subject. The impotence caused by disease may, in time, disappear, especially if the ravages of the disease have not destroyed the germ cells, as is often the case. An impotence ascribed to psychical causes may rarely occur, but concerning this factor, we have, obviously, little or no exact evidence.

The sterility induced in crossing animals and plants belonging to different varieties and species has long been known. The early hybridists of plants, Gärtner, Kölreuter, Nägeli, Gordon and others, were familiar with the frequent failure of pollen, placed upon the stigma of certain plants, to produce seed in the ovules of that plant, and with the fact that even if seed is obtained, it may not grow when planted. Kölreuter and Gärtner saw in sterility the criterion whereby species may be distinguished. If two forms bred together produced seed, and the seed was capable of growing into perfect plants, the two forms were considered as belonging to the same species. If, on the other hand, no seed was produced, or if produced, this seed was incapable of growth, the two forms were considered as belonging to distinct species. However, as Darwin points out, these two workers were biased in their appreciation of sterility, as a valid criterion for distinguishing species, for they themselves, as have indeed all workers since them, described all degrees of sterility under such circumstances, from slight deviations in form of the hybrid plants, through a condition where the seed, although formed, was shrivelled and incapable of producing the young plant, to complete sterility, where no indication of even a pollen-tube is seen in the style of the pistil. Obviously, the personal equation of the experimenter will be a potent factor in determining whether there were two species, or a single one involved in questionable cases, and the definiteness of the criterion is largely detracted. To Darwin, who had carried out thousands of crosses, the use of sterility as a distinguishing character for species was an impossibility, and this fact was utilized by him in combating the criticism urged against the theory of natural selection, that it could not account for the origin of sterility by assuming that it was a factor in isolating species.

---

[1] Presented at the fourth evening seminar of the Harpswell Laboratory, August 2, 1910.

It has been only within comparatively recent times that an understanding has been reached as to what are the intimate results of sterility. It is true that Gärtner knew that the pollen of many hybrids was shrivelled and functionless, but farther than this, nothing was known of the condition of the spore-bearing and gamete-bearing parts; for the rôle of the pollen-tube, with the nuclei contained, and of the ovum in the ovary was as yet unknown and the discovery of the alternation of generations in the higher plants had not been made. Not until the reduction of the tetrads had been worked out was it possible to understand the failure of the hybrid to produce seed, or, if seed were produced, to understand why abnormalities occurred in the young hybrid plants.

We have spoken thus far mainly of the work of botanists, for the reason that little or nothing has been accomplished by zoologists until recently, which throws light upon the problem of sterility. It was known by Aristotle that species would cross and that the offspring varied from the parents in vigor and in other characters. If the etymologists inform us correctly, the word leopard, compounded of *Leo,* lion, and *Pardos,* panther, or tiger, points to a belief among the Greeks, that the leopard was a cross between the lion and tiger. The knowledge that captive animals bred only rarely, many not at all, and that even when mating occurred, the act was functionless and no offspring resulted, although the animals were apparently normal, is nothing of recent date. As to why offspring are not produced under these conditions, we are wholly ignorant. No one has determined whether the male actually conveys the fertilizing fluid to the female and if so, whether functional spermatozoa are present. It is known that in some cases, confinement of wild animals induces degeneration of the internal generative organs. Psychic causes, too, are undoubtedly present, inhibiting the mating instinct, but these factors are so subtile that they defy analysis. The data are familiar to every keeper of zoological gardens, and yet no attempt, to my knowledge, has been made to determine any of the details involved.

Several cytologists have examined the gonads of hybrid animals with a view to determining the condition of the sex cells. Thus, Guyer studied the crossed pigeons from the cotes of Professor C. O. Whitman at Chicago and found great abnormalities in the secondary spermatocytes, such as clumping of the chromatin, degeneracy of the cells as a whole, tri- and other abnormal mitoses. Spermatozoa were formed in many cases, but these cells were obviously abnormal and pathologic. The gonads of the mules obtained by crossing canaries and English goldfinches, siskins, bullfinches, etc., are degenerate, and in some cases which I have examined no trace of gonad could be found.

The cytology of the gonad of the mule obtained by crossing the mare with the jackass has been examined by H. E. Jordan who describes the testis as follows:

> The seminiferous tubules are lined with Sertoli cells, spermatogonia and a few primary spermatocytes in early stages. The nucleus of the latter appears to be in the spireme phase of the contraction stage and in process of regressive change. Mitoses are exceedingly rare and those

present are seen among the basal cells. Nothing corresponding to a secondary spermatocyte or a spermatid can be found, nor are spermatozoa anywhere present, either in the seminiferous tubules or the epididymis. The absence of spermatozoa explains why mules are infertile *inter se,* as also the fact that no issue results from a cross between a female horse and a male mule (the cross between a female mule and a stallion is known to have resulted in offspring).[2]

Aside from this study, and that of Guyer spoken of above, I know of no examination which has been made of the gonads of hybrid vertebrated animals. The conditions which I have found in canaries resemble closely those found by Guyer, in pigeons. The observations of Ancel and Bouin[3] on cryptorchid horses resemble to quite an extent, those by Jordan upon the mule testis.[4]

Hybridization experiments with lower forms of animals throw some light upon the behavior of the germ cells concerned in fertilization. Moenkhaus found that he could cross *Fundulus* and *Menidia,* two species of fishes, and obtain normal hybrids. Owing to the differences in size of the chromosomes in the two species, he was enabled to determine the fate of the chromosomes of the egg and of those of the spermatozoon and it was possible to follow them through the embryonic history, through the various mitoses of segmentation and later. Here, the chromosomes were in no way antagonistic and proceeded through the mitoses side by side.

Balzer[5] performed a series of very interesting experiments upon several species of echinoderms occurring in the Bay of Naples. He used four species, *Strongylocentrotus, Echinus, Arbacia* and *Sphærechinus,* making reciprocal crosses. Crosses between *Strongylocentrotus, Echinus* and *Arbacia* gave normal fertilizations, with no loss of chromatin in the earlier segmentation anaphases, and the plutei exhibited normal skeletons, except

---

[2] Whitehead, R. H., 1908, "A Peculiar Case of Cryptorchism and its Bearing upon the Problem of the Function of the Interstitial Cells of the Testis," *Anatomical Record* (Philadelphia, U. S. A.), Vol. 2, p. 177.

[3] Ancel et Bouin, 1903 4, *Journ. de Physiol. et de Path.,* T. 6, Nr. 6, 7. Also *Comptes Rendus,* T. 137, Nr. 26; T. 138, Nrs. 2. 3. 4.

[4] See Schwalbe, E. (Herausgeber), "Die Morphologie der Missbildungen des Menschen und der Tiere," Ein Hand- und Lehrbuch, Dritter Theil: Die Einzelmissbildungen.

[5] Balzer, F., 1909, "Ueber die Entwicklung der Echiniden-Bastarde mit besonderer Berücksichtigung des Chromatinverhältnisse," *Zool. Anz.,* Bd. 35, S. 5.

in one case. With *Sphærechinus* and *Strongylocentrotus* several chromosomes were eliminated in the anaphase of the first segmentation stage, which were excluded from the nucleus of the resulting cells, when the nuclear walls were formed. Correlative with this, the plutei showed abnormalities and the general resemblance was to the maternal species. Apparently here the case is different from that of Moenkhaus's *Fundulus-Menidia* hybrids, for the chromatin of the egg in part at least, is not adapted to association with that of the eggs of the other species. If this interpretation is correct, we may refer the abnormalities of the hybrid produced from the cross of *Sphærechinus* to the loss, during the segmentation stages, of chromosomes derived from the female. The analysis cannot be pushed farther back, in this case, for we are unable to understand why these chromosomes which are excluded from the reconstructed nucleus are "incompatible" with those of the egg-nucleus. Whatever the cause, it is probably similar to the agglutinization of erythrocytes, spermatozoa, bacteria and other cells in the fluids from other organisms or in artificial media. In this connection, it is interesting to recall that Guyer and Jordan found the abnormalities in the testes of hybrids appearing first during the synapsis period, when the chromosomes from paternal and maternal sources conjugate two-by-two, either end-to-end or side-by-side (probably side-by-side in chordates, according to the observations of Winiwarter). Recent study of spermatogenesis and oogenesis points to the conclusion that the maternal and paternal chromosomes remain distinct and more or less isolated from one another in the primary germ cells, from the time of fertilization until synapsis, and then for the first time are they intimately associated into pairs, as Montgomery suggested —a view which has been abundantly confirmed by Sutton, Stevens, Wilson, and a number of others. Here, then, would it be expected that incompatibilities, if ever present, would become apparent. If the phenomenon is of the same category as agglutinization, hemolysis and the like, it should be possible to render the sex-cells of one animal immune to the lytic action of those of other animals, on the principles of immunization and antibody development. In a case, however, where such a relation appears much more clearly, it seems that the phenomena are not of the same kind. I refer to the auto-immunity of *Cynthia*, where the eggs of a given individual of *Cynthia partita* cannot be fertilized by the spermatozoa of the same individual. Morgan analyzed the phenomenon in the light of immunity and was unable to demonstrate a parallel between the *Cynthia* immunity and that in anti-body formation.[6] However, the case described by Morgan may not be equivalent to those of hybridization experiments, such as we have described.

Concerning the relation of the chromosomes to fertilization and subsequent condition of the embryo, Bataillon[7] derives certain evidence from his amphibian crosses for the conclusion that the number of chromosomes in the two parent species involved in the cross is of importance in determining the condition of the embryo resulting. Thus, when the number of chromosomes in the two species is the same, no embryo results, while crosses between species with different numbers of chromosomes lead to progeny. If this observation is true, it might be due to the fact that mainly, or only those chromosomes which are in excess of the number occurring in the species with smaller number of chromosomes and which do not pair up in synapsis with the chromosomes of that species, are functiónal in producing the embryo. Under these conditions, we should expect that the embryo would resemble the species with the greater number of chromosomes. However, this does not follow, inasmuch as Bataillon did not observe nuclear copulation, but rather a mode of artificial parthenogenesis is supposed to occur, the male element being wholly without effect in inducing fertilization and, therefore, the progeny would resemble the maternal species.

In 1906, Emil Godlewski, Jr., succeeded in obtaining a few hybrids between the sessile crinoid, *Antedon* ♂ and *Echinus* ♀, thus involving two classes of echinoderms, the Echinoidea and Crinoidea. The sperm exerted a marked inhibition of development as a whole and the hybrids resembled the maternal *Echinus*. This case is probably similar to the one described above where non-compatibility is evident between egg and sperm nuclei in fertilization. Godlewski did not examine the chromosomes with a view to determining their condition in the cells of the hybrids.

[6] Morgan, T. H., 1910, "Eggs of *Cynthia*, Immune to their own Sperm," a paper before the Society for Experimental Biology and Medicine, to be published in full in the *Journal of Experimental Zoology*.

[7] Bataillon, M. E., "Le substratum chromatique héréditaire et les combinaisons nucleaires dans les croisements chez les Amphibiens." *Comptes Rendus*, Paris, T. 147, f. 692.

Godlewski did not find it necessary to resort to artificial means in causing the spermatozoon of *Antedon* to penetrate the egg of *Echinus*, but by an ingenious method Loeb[8] was enabled to cause the egg of a member of one phylum to be fertilized by the spermatozoa from a member of a different phylum. Kupelweiser[9] afterwards applied Loeb's method to a cross between the mussel, *Mytilus* ♂, and the echinoderm, *Echinus* ♀, the method involving a subjection of the eggs to a hypertonic solution of sea-water, as in artificial parthenogenesis. Bataillon[10] believes that only artificial parthenogenesis is operative in this case, basing his conclusions partly upon analogous crosses in amphibians, where he has crossed *Triton* ♂ with the toad *Pelodytes* ♀, and observed that no sperm asters formed and segmentation proceeded without any participation on the part of the sperm nucleus.[11] Of course if Bataillon's contention is correct, the case is of no interest in the present connection, but if the two cases are not parallel, Loeb has overcome what we may grossly term sterility, by artificial means, by modifying the osmotic pressure and the permeability of the egg-membrane so that the spermatozoon of the foreign species may enter. Sterility here then may be due to purely mechanical factors. Yatsu has pointed out that the failure to procure crosses between the frogs *Rana sylvatica* ♀ and *Rana virescens* ♂ is due to the fact that the heads of the spermatozoa of the latter are too large to enter the eggs of the former. Here, again, a purely mechanical factor is involved.

While no experiments have been performed to my knowledge to determine whether a kind of acclimatization may be induced in hybrids, yet some experiments performed by botanists shed some light upon this point. Gärtner,[12] Wichura[13] and Nägeli[14] believed that fertility decreased in later generations, but Naudin,[15] C. C. Hurst[16] and others, including DeVries,[17] believe that fertility increases, or, in other words the barrier, more or less perfect, between hybridization of the species involved, is gradually broken down. As Kerner[18] has shown, indeed, many hybrid plants are more fertile than the parent species and this is maintained and increased during future generations, so that the hybrids have replaced the parent species. There is, then, a basis for believing that a kind of acquired "congeniality" obtains, whereby the conjugating cells become more compatible, whatever this may ultimately involve. An interesting case was described by Gordon[19] where *Nicotiniana, Digitalis* and other hybrids are sterile *inter se,* but fertile with the parent forms. In the cross between the dog and the wolf, sterility begins, not in the earlier generations, but in later ones, according to the observations of Flourens, but as Darwin remarks, it is doubtful that this is due to increasing sterility because of crossing, but rather to confinement or, indeed, to inbreeding.

---

[8] Loeb, J., *Roux's Archiv*, Bd. 26, Heft 3.

[9] Kupelwieser, H., *Roux's Archiv*, Bd. 27, S. 434.

[10] Bataillon, E., "L'imprégnation hétérogène sans Amphimixie nucléaire chez les Amphibiens et les Echinodermes (à propos du recent travail de H. Kupelwieser)," *Roux's Archiv*, Bd. 28, S. 43–48, 1909.

[11] Bataillon, E., "Imprégnation et Fécondation," *Comptes Rendus*, 11 Juin, 1906.

[12] Gärtner, 1849, "Bastarderzeugung im Pflanzenreich."

[13] Wichura, M., 1865, "Die Bastardbefruchtung im Pflanzenreich."

[14] Nägeli, C. v., 1866, "Botanische Mittheilungen," *Sitz. ber. der Münch. Akad. Wiss.*, 13 Jan., 1866.

[15] Naudin, Ch., 1869, "Nouvelles recherches," *Nouvelles Archives du*

The students of plant cytology were the first to examine critically the structures concerned in reproduction in hybrids. Gärtner long ago observed the shrivelled pollen grains, as we have said before, but that was before the modern cytological methods came into use. Jančič[20] has contributed widely to this department of research. He observed that the number of pollen grains decreased in certain hybrid plants and that in the several species he examined, this numerical reduction occurred in approximate amounts to one fourth, one half or three fourths the average number of grains. Moreover, cytological examination of the anthers showed that many of the nuclei after reduction of the tetrads were atrophied, and the conclusion is obvious that herein lies the explanation of his numerical ratios mentioned above; for in some crosses, three fourths of the nuclei destined for the pollen (the daughter and granddaughter cells of the pollen mother-cell), or, in other words, three of the four tetrads, aborted, leaving but one to become pollen (hence the one fourth), while in other cases, two of the tetrads disappeared (two

---

Muséum a'histoire naturelle, Paris.

[16] Hurst, C. C., 1900, *Journ. Roy. Hortic. Soc.,* Vol. 24, p. 124.

[17] De Vries, H., 1903, "Die Mutationstheorie," Vol. 2, p. 66.

[18] Kerner, A. von, "Können aus Bastarden Arten werden?" *Oesterr. Bot. Zeit.,* Bd. 21, 1871.

[19] Gordon, D. A., 1862, *Mem. Acad. Stanisl.,* p. 228.

[20] Jančič, A., "Untersuchungen des Pollens hybrider Pflanzen," *Oesterr. bot. Zeitschr.,* 1900, Nr. 1, 2, 3.

fourths), so that one-half of the normal number of pollen grains appeared. Here, again, it is the period of synapsis or of conjugation of the maternal and paternal chromosomes (the stage corresponding to the gametophyte, where the chromosomes are reduced in number) where the effects of hybridization are evident.

Juel[21] has shown that the chromatin distribution in the nuclei of hybrids is irregular, corresponding to the conditions in hybrid animals described earlier in the present paper. The condition of the chromosomes during actual synapsis is such that it is impossible to observe their behavior directly and, doubtless, nothing could be learned of the ultimate cause of the irregularities through mere observation during these periods, even if the chromosomes could be more clearly followed. In such cases, it seems to me, we have fought the matter of sterility to its inner keep, and until experimentation comes to our aid, we shall be able to proceed no farther. "Über die Art und Weise, wie die Eizellen steril werden, haben wir keine erwähnenswerthen Angaben gefunden" (DeVries).

Several cytologists have taken advantage of the exhaustive studies of DeVries upon hybrids of the primrose, *Œnothera lamarckiana*, to study the cellular phenomena of crosses whose general features are well known. Thus, Geerts[22] has recently studied the partial sterility and the development of the embryosac of *Œnothera* and finds that there are no antipodal cells developed and that the endosperm forms from the pole cells. Sterility, says Geerts, is a matter of irregularities in the reduction division and therefore his observations tally with those, both plant and animal, spoken of above.

Gates[23] and Miss Lutz[24] have investigated the cytology of *Œnothera* crosses and of *Drosera* hybrids. Irregular distribution of the chromosomes obtained in the reduction division and these differences are correlated with the external characters of the crosses.

---

[21] Juel, H. O., "Beiträge zur Kenntnis der Tetradentheilung," *Jahrb. wiss. Bot.*, Bd. 35, 1900.

[22] Geerts, J. M., "Récueil Trav. Bot. Néerl.," T. 5, 1909.

[23] Gates, R. R., *Bot. Gaz.*, Vols. 46 and 48; *Science*, Vols. 27 and 30; *Archiv für Zellforsch.*, Bd. 3, H. 4, 1908–09.

[24] Lutz, Annie M., *Science*, Vol. 29, 1909.

Finally, Rosenberg[25] has invaded this fascinating field and studied the hybrid sundews exhaustively. The main results of his observations are similar to those given above in the case of the other workers. Rosenberg adopts the explanation of "Unverträglichkeit" (incompatibility) for the behavior of the chromosomes—a view which Tischler,[26] who speaks from much experience in the cytology of hybrids, believes to be inadequate, for the reason that, as Rosenberg as well as he himself shows, there are a few cases where typical embryo-sacs are developed and indeed the *anlage* of the young sporophyte may be found. "Die gewöhnliche Sterilität nicht in einer Unverträglichkeit der beiderelterlichen Chromosomen liegt."[27]

We are able to see, therefore, that sterility, as far as may be judged from studies upon the germ cells which have been made thus far, is a matter of the fundamental constitution of the organism. It concerns the bearers of hereditary traits, the chromosomes. All of the studies which have been made point to the conclusion that whatever may be its nature, there is an "incompatibility" existing between the chromosomes of individuals of different species or varieties. Tischler's contention seems to me to be ill-founded, for the cases where normal structures occur in the embryo-sacs of these hybrid plants are exceedingly few, and when we consider the observations of other workers upon plant material, and of the animal cytologists we find abundant reason to believe that the exceptions mentioned by Tischler may be better explained in another way. Moreover, we know nothing of the constitution of the nuclei of the cells of the young sporophytes, with respect to the mingling of maternal and paternal chromosomes. It may be, indeed, as Gates has suggested, that a condition of apogamy may obtain.

Undoubtedly the next few years will see many points as yet undetermined, brought into proper perspective and we shall be able to give a more complete account of the rationale of sterility.

MAX MORSE.

---

[25] Rosenberg, O., "Cytologische und morphologische Studien an *Drosera longifolia* by *rotundifolia*," *K. Vetenskaps Akad. Handl.*, Bd. 43, Nr. II., 63 S. Stockholm.

[26] Tischler, G., *Zeitschr. f. ind. Abstammungsl.*, Bd. 3, H. 3, 1910.

[27] Tischler, *l. c.*

NOTES AND LITERATURE

NOTES ON ICHTHYOLOGY

An elaborate and excellent monograph is the "Ichthyologia Amurensis," by Dr. Leo S. Berg, being a "Catalogue of the Fishes of the Amur River," entirely modern in its method, and very accurate in its details. Unfortunately, most of this admirable volume is in Russian, without résumé in any modern language. It is published by the Imperial Academy of Sciences at St. Petersburg, volume 24.

Professor T. D. A. Cockerell, of the University of Colorado, continues his very interesting and fruitful studies of the scales of fishes. In the *Proceedings of the Biological Society of Washington* (1910), he discusses the scales of the Cyprinoid and Clupeoid fishes. He shows that the American genera related to *Chondrostoma* are but two in number, *Orthodon* and *Acrocheilus.* The scales of the American species are less primitive than those of the old-world *Chondrostoma.*

In the study of the scales of *Leuciscus* and *Rutilus,* Professor Cockerell shows that none of the American species belong to either of these two genera, and none of them to the genus *Phoxinus.* For the American species called *Leuciscus,* the name *Richardsonius* of Girard should be adopted; and for the American species called *Phoxinus* the new subgeneric name *Margariscus* is suggested. The name *Myloleucus* of Cope is properly adopted for the American species hitherto called *Rutilus.* A new subgenus, *Temeculina,* is proposed for *Richardsonius orcutti.* The Japanese species called *Leuciscus* are not related to the European species, but approach more nearly to the American forms, perhaps entering the genus *Richardsonius.* Mr. Cockerell shows that the genus *Notemigonus* is well separated from the European genera *Abramis* and *Blicca.*

The scales of the herring-like fishes are also discussed. These show relatively simple and primitive structure.

The scales of the Atherinoid fishes show qualities more or less like those of the mackerels. In other papers published in the *Smithsonian Miscellaneous Collections,* volume 56, Mr. Cockerell discusses the scales of the African Mormyrid fishes and of the African Characins.

In the *Proceedings of the Royal Society of Victoria* (1909), Miss Ethel R. Morris and Miss Janet Raff discuss the structure of the little lancelet of the coast of Victoria, which they call *Asymmetron bassanum.* The generic name *Epigonichthys* of Peters has priority.

In the *Journal of the Royal Society of New South Wales,* Vol. XLI, Mr. H. C. Dannevig, of the Department of Fisheries, discusses the effects of the coastal winds of Australia on the abundance of fish in inshore waters. He shows that the relative abundance of many species in different places is due to the nature of the winds.

In the *Annals of the Carnegie Museum,* Volume V, Dr. Charles R. Eastman describes a new fossil shark, *Helodus comptus,* from Meadville, Pa.

In the *Annals and Magazine of Natural History,* Series 8, Vol. 4, Mr. C. Tate Regan describes a number of new species of fishes, mostly eels, from the South Seas and Australia.

In the same journal, Mr. Regan discusses the three-spined sticklebacks of the world. He finds those of the Atlantic coasts of Europe and America and those of the Pacific coast alike, including all the species of three-spined sticklebacks hitherto described under the name of *Gastrosteus aculeatus,* with the exception of *G. algeriensis,* which has a smaller number of vertebræ, 29 instead of 31 to 33. He also describes a species with a slender snout, from Rome, under the name of *Gastrosteus hologymnus,* and a new species, *Gastrosteus santæ-annæ,* from the Santa Ana River in California. This he regards as distinct from the naked specimens of *Gastrosteus* hitherto known as *G. williamsoni,* by the presence of 29 instead of 32 vertebræ. The specific distinction of *G. santæ-annæ* is very doubtful, but Mr. Regan is doubtless correct in saying that mailed, half-mailed and naked forms in Europe and America are the same species, those living in the sea being fully mailed, those living in fresh water mostly naked.

In the same *Annals,* Mr. Regan discusses the caudal fin of *Elops* and of other fishes. He finds the tail of *Elops* distinctly heterocercal, like that of some of the fossil forms of earlier periods. He also shows that the tail of *Fierasfer* is not gephyrocercal. In its general structure, it is like that of related forms, but the caudal fin has disappeared.

In the *Proceedings of the Zoological Society of London* for

1909, Mr. Regan discusses in detail the family of Anabantidæ.

In the *Archives de Zoologie Experimentale,* fifth series, volume 1 (1909), Dr. Louis Fage discusses in great detail the variations in the red surmullet of Europe. He finds that *Mullus surmuletus* is a form of *Mullus barbatus* somewhat less developed, so that the two species can not be maintained as distinct. If one is to give the right value to the variants of the surmullet, it is necessary to have not only a trinomial but a quadrinomial system of naming.

In the *Bulletin de la Société Philomathique,* 1909, Dr. Jacques Pellegrin discusses the minute catfish of the genus *Vandellia.*

In the *Proceedings* of the Seventh International Zoological Congress, Mr. Regan discusses the origin of the Chimæroid fishes. He regards them as derived from the same stock as the sharks, but more primitive.

In the said *Proceedings,* Mr. Regan discusses very fully the classification of the Teleostean fishes. It will be a long time before any satisfactory grouping of these animals can be made, but every analysis of this sort shows the importance of the problem, and the soundness of the American view, that a complete analysis of these forms must be made before any satisfactory synthesis is possible. To place groups together simply because we don't know how to separate them, does not form a classification of any permanence. A new order, Malacichthyes, is made for the genus *Icosteus,* and another order, Chondrobrachii, for *Podateles.* On the whole, this classification shows several points of advancement over any previously proposed, but there is plenty of room for doubt in regard to many of the adjustments.

In the "Scientific Investigations of the Fishes of Ireland," Volume 4, E. W. L. Holt and L. W. Byrne discuss the *Chimæras* of the Irish coast. These are three in number, *C. monstrosa, C. affinis* and *C. mirabilis. C. plumbea* and *C. abbreviata* are identical with *C. affinis.* A new species of *Rhinochimæra, R. atlantica,* is described. Of this genus, only a single Japanese species is hitherto known.

In the *Quarterly Journal of Microscopical Science,* volume 54 (1910), Professor J. Graham Kerr describes the development of the alimentary canal in *Lepidosiren* and *Protopterus.*

In the *Publications of the Department of State,* the International Fisheries Commission (David Starr Jordan and Edward Ernest Prince) have published the regulations, sixty-six in number, by which it is proposed to control the fisheries of the international boundary waters.

In the *Proceedings of the United States National Museum,* Dr. Jordan and William Francis Thompson describe a new species of deep-water sculpin, *Triglopsis ontariensis,* from Lake Ontario. The Lake Michigan form related to this, long since named *Triglopsis stimpsoni,* is also described and figured.

In the same *Proceedings,* Frank Walter Weymouth, of Stanford University, describes a collection of fishes from Cameron, Louisiana. One species, *Leptocerdale longipinnis,* is described as new. The three related species of this family, Cerdalidæ, are known from the west coast of Mexico.

In the "Smithsonian Report" for 1908, Dr. Theodore Gill discusses the variant forms of angler fishes, with figures of many species. He shows that the name *Lophiodes,* Goode and Bean, "Oceanic Ichthyology," p. 537, has priority over the name *Chirolophius.*

In the *Proceedings of the Portland Society of Natural History,* Vol. II, William Converse Kendall gives a list of the fishes of Labrador, as collected by the Bowdoin College Expedition of 1891. A check list of the species of Labrador contains seventy-three names.

In the *Bulletin of the Illinois State Laboratory of Natural History,* Professor Stephen A. Forbes gives a series of maps, showing the distribution of the fishes of Illinois in the streams of the state. The distribution of these fishes reflects, as Professor Forbes says, in uniformity and relative monotony, the features of the topography of the state.

In the *Philippine Journal of Science,* Vol. IV (1909), Mr. Alvin Seale describes a large number of new species of fishes from the Philippines, in addition to those named in the check list of Jordan and Richardson, published at about the same time in the same journal. Mr. Seale has had opportunities for making studies of the Philippine species such as have fallen to no other ichthyologist.

In the *Bulletin of the Bureau of Fisheries,* Vol. 28, are the proceedings of the Fourth International Fisheries Congress, held at Washington in September, 1908. Upwards of thirty papers bearing on fisheries are contained in this series, covering in some degree almost every matter of interest to fish culturists.

Notable among these papers is one by Dr. Theodore Gill, on a plea for exact observation of the habits of fishes as against undue generalization.

Mr. L. F. Ayson discusses the introduction of American fishes into New Zealand, an operation which has been thoroughly successful. Most notable is the growth of the rainbow trout in the lakes of the northern island. Anglers are restricted to thirty pounds a day, and over twenty tons of trout have been taken out of two small lakes at Rotorua in one season. The rainbow trout is frequently taken from ten to twenty pounds or more in weight.

Mr. G. M. Dannevig discussess the success of the Norwegians in the planting of the fry of codfish in depleted waters.

Three papers, by S. W. Downing, Frank N. Clark and Paul Reighard, on the promotion of whitefish production in the Great Lakes, are especially important and suggestive. It is shown that with the adequate planting of whitefish eggs it would be possible practically to capture all the adult fish, and the natural spawning of the fish could be made a matter of no importance. This discussion looks forward to the time when the fishing season for whitefish will be largely identical with the spawning season; that is, in November, when the eggs of each fish thus caught will be preserved and hatched, and the young fish placed in the open water of the lakes. The whitefish ground is greater in Lake Erie than in any other of our American lakes. The plant of whitefish fry in Lake Erie now approaches one billion young fish per year, and, in spite of the enormous fishing taking place in that lake, the number of whitefish is increasing.

The following are the special recommendations of Mr. Reighard, and these should receive the most careful consideration from those interested:

1. It is recommended, as a result of the foregoing study, that the output of whitefish fry be increased as rapidly as possible, as affording the most certain means of increasing the whitefish production.

2. That an intensive plant of at least one hundred fry per pound of whitefish caught be made on depleted areas. (Lake Ontario and the southern waters of Lake Michigan are in need of especial attention.)

3. That a close season be observed during the breeding season of the whitefish as at present, but only for such waters as are not under federal control.

4. That commercial fishing with pound nets and seines be permitted in the waters of the Great Lakes during the breeding season of the whitefish wherever the state or national authorities are prepared to undertake to care for the spawn of the fish taken; the fisherman to be under legal obligation to permit the use of the fish taken by them for the purpose of spawn-taking.

5. It is suggested that central control of the fishing operations of the Great Lakes is highly desirable. Whether this is possible in American waters through federal control or through concerted action of the states is a question that can not be discussed here. A central control, under which fishing grounds should be leased and fishermen licensed, would, if properly administered, reduce the cost of fishing and make possible more extended artificial propagation. The central authorities should have power to modify the fishing regulations pending legislative action. Such a system might be made self-supporting.

6. The need of more exact knowledge of the habits of the whitefish and of all the conditions under which it lives is very evident. In the interest of the fisheries these matters should be subjects of investigations to be carried on under federal auspices, with suitable equipment and for a long period of years.

In another paper, President Jordan discusses the work of the International Fisheries Commission, outlining the proposed operations of Great Britain and the United States. This commission at that time had just been appointed.

John I. Solomon discusses a process for preserving the pearl oyster fisheries, and increasing the value of the yield of pearls. To this important contribution was awarded the prize of $100, by the New York Academy of Sciences.

Professor Shinnosuke Matsubara, of the Imperial Fisheries Institute of Tokyo, discusses the variant forms of the goldfish developed by Japanese artist breeders. These are illustrated by colored plates.

Professor Jacob Reighard, of the University of Michigan, gives a most valuable account of the nests of the horned dace, and of the methods by which the habits of fresh-water fishes can be effectively studied.

David Starr Jordan.

THE MAMMALS OF COLORADO

Colorado Mammals.[1]—About seven years ago I called on Mr. E. R. Warren at Colorado Springs, and saw his collection of mammals, then recently begun. It was a small affair, easily laid out on the parlor table. Since then, Mr. Warren has labored unceasingly, visiting many different parts of Colorado, and has accumulated an immense series of skins. The collection soon outgrew its original quarters, and is now housed in a special building, in numerous cabinets which are already overcrowded. While mainly a Colorado collection, it includes many species from other parts of the country, obtained in exchange. Mr. Warren has not only collected all these materials for taxonomic investigations, but has paid much attention to the habits of the animals, and in particular has secured a splendid set of photographs showing them in their native haunts. The logical outcome of all this excellent work, a book on Colorado mammals, has just appeared. It contains descriptions of all the species and subspecies known to inhabit the state, with numerous illustrations, showing the living animals and the skull of each genus. It is so far technical that it contains exact descriptions and all other details needed for precise classification and identification, but each form is also discussed in a popular manner, often with entertaining anecdotes. Heretofore the study of Colorado mammals has seemed too difficult for any one not a specialist, but with the aid of this book it is made easy for any intelligent person, or as easy as such a subject, from its nature, can be. The only regret I have about the work is that there is not more of it: I should have liked a chapter on fossil mammals (especially of the later periods), and one on parasites of mammals.

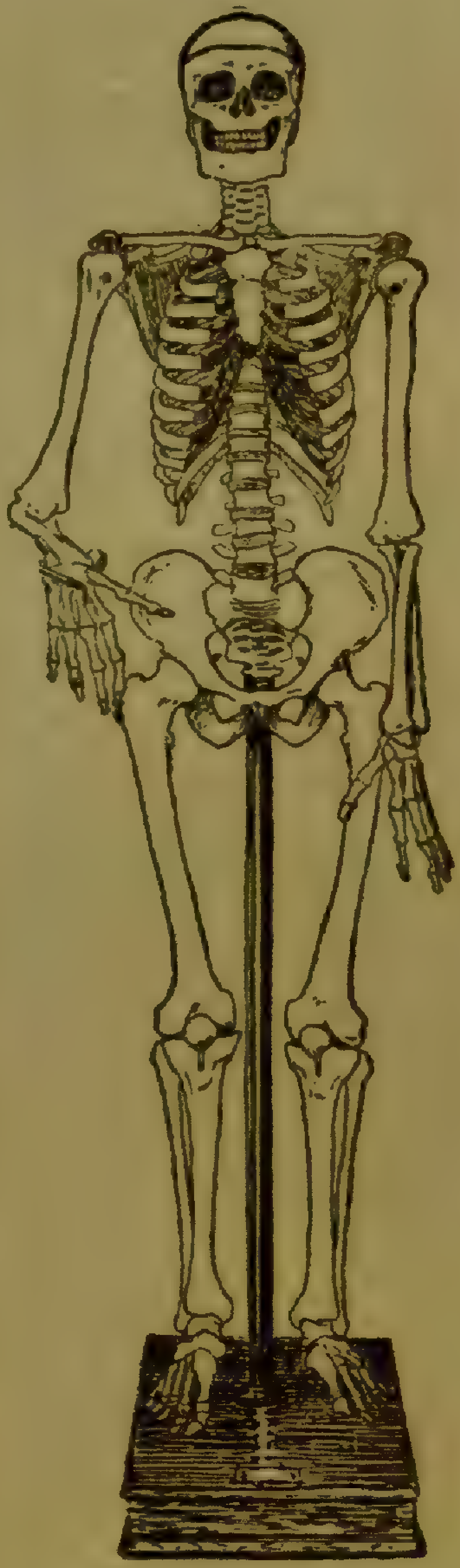
Apart from my great pleasure in the book itself, I can not other than regard the manner of its production as a good omen. Mr. Warren has lately been appointed honorary curator of Colorado College Museum, but he is essentially an amateur, in the best sense of that word. He resembles the numerous amateur naturalists of England, who have done so much for science; like them, he has labored for the love of the work, without recompense, and has shouldered the expense of publication, heavy as it must have been. The most modest of men, I fear he may resent being called a benefactor, yet it would be hard to exaggerate the benefit to the community which might come from an increase of the spirit he represents. T. D. A. Cockerell.

---

[1] "The Mammals of Colorado," by E. R. Warren, G. P. Putnam's Sons, New York, 1910.

The Anatomical Laboratory of Charles H. Ward

189 West Avenue, Rochester, N. Y.



OUR HUMAN SKELETONS are selected specimens scientifically prepared and mounted. They are undoubtedly the finest and strongest skeletons obtainable, and are purchased by the leading Medical and Literary Colleges, Schools, Surgeons, etc. We make a number of special skeletons for demonstrating dislocations, muscular areas, anthropometric landmarks, muscles, etc.

The mounting of the articulations permits movements as in life. Strength and rigidity are secured by the use of a special bronze wire of enormous tensile strength and great resistance to oxidation. Portability and ease of demonstration are attained by our nickeled steel clutch standard, which is a great protection as well.

These skeletons are shipped entirely set up, carefully wrapped, and with detailed directions for unpacking and handling. Our Catalogue gives further details.

OUR SKELETONS OF TYPES OF VERTEBRATES are large specimens, principally of American species, mounted in characteristic poses on polished mahogany pedestals, with nickel-plated brass standards. We offer a type collection for schools and colleges.

ANATOMICAL MODELS

Besides importing duty free for educational institutions we manufacture anatomical models in great variety. These have been purchased by many Schools and Universities. The series includes complete torso, head, brain, nervous system, greatly enlarged models of the sense organs, etc., of most of which we have large half tones. These models pay no duty, no transportation, no middlemen's profits, but are sold direct, at very moderate prices, and can be supplied **promptly when needed.**

We also make **BIOLOGICAL MODELS** of the forms commonly dissected in the laboratory. These models represent complete dissections of the various animals, greatly enlarged (frog 18 inches long, etc.), mounted upon ebonized pedestals, with detailed descriptive labels. Series includes Coral, Sponge, Medusa, Starfish, Diatoma, Leech, Earthworm, Clam, Crayfish, Amphioxus, Perch, Frog. Sample labels and halftones on request.

ANTHROPOLOGY AND ETHNOLOGY

The Finsch Life Masks of Aborigines, including those islanders recently acquired by the United States. Casts of Skulls, Skeletons and Brain, of Prehistoric Man. Casts of prehistoric bone carvings from the caves of France. Stone implements of the North American Indians.

RELIEF MAPS OF THE UNITED STATES, the Continents, Grand Cañon of the Colorado, Yosemite Valley, etc., made in Washington, D. C., for the United States Geological Survey and others by Howell (a former member of the Survey). **The only authoritative relief maps made commercially in America.** They are light, strong (made of papier maché), beautifully colored and lettered, and as low in price as "cheap" maps. For catalogues, halftones of models, maps, etc., address

CHARLES H. WARD

189 West Avenue, Rochester, N. Y.

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE APRIL NUMBER

The Origin of the Electricity Tissues in Fishes. Professor ULRIC DAHLGREN.

The Material Basis of Mendelian Phenomena. Dr. REGINALD R. GATES.

Mendelian Phenomena without de Vriesian Theory. Dr. W. J. SPILLMAN.

The Evolution of New Forms in Viola through Hybridism. Professor EZRA BRAINERD.

Tertiary Archhelenis. Dr. A. E. ORTMANN.

Shorter Articles and Discussion: The Probable Origin of the Crinoidal Nervous System: AUSTIN H. CLARK.

Notes and Literature: The Question of Sex Determination: Professor H. E. JORDAN. Recent Investigations on the Comparative Anatomy of Conifers: Professor E. C. JEFFREY.

CONTENTS OF THE MAY NUMBER

A Review of Some Recent Criticisms of the Restorations of Sauropod Dinasaurs. DR. J. W. HOLLAND.

Anatomical Characters in the Evolution of Pinus. IRVING W. BAILEY.

Facts about the "Lobster Pearl." Professor FRANCIS H. HERRICK.

Shorter Articles and Discussion: An Eighteenth Century Microscope, Professor BASHFORD DEAN. Stomatolepas, a Barnacle Commensal in the Throat of the Loggerhead Turtle. HENRY A. PILSBRY. The Age of Speed Sires, CASPER L. REDFIELD.

Notes and Literature: *Biometrics*—Recent Quantitative Studies in Variation in Social Insects, DR. RAYMOND PEARL. *Experimental Zoology*—The Effects of Extirpation and of Transplantation of the Reproductive Organs in Insects, E. N. BROWNE. Wheeler on Ants, Professor G. H. PARKER.

CONTENTS OF THE JUNE NUMBER

The Botanical Society of America:
The Nature of Physiological Response. The Late Professor CHARLES R. BARNES.

The Place of Plant Responses in the Categories of Sensitive Reactions. Professor FREDERICK C. NEWCOMBE.

The Larva and Spat of the Canadian Oyster. Dr. J. SAFFORD.

The Alimentary Canal of a Carboniferous Salamander. Dr. ROY L. MOODIE.

Shorter Articles and Discussion: Observations on the Spawning Habits of Hydroides Dianthus. Professor CHARLES W. HARGITT.

Notes and Literature:
Protozoa—Doflein's Lehrbuch der Protozoenkunde: Professor CHARLES A. KOFOID. Celebrating Darwin's Greatness and Darwinism's Weakness, V. L. K.

CONTENTS OF THE JULY NUMBER

A Consideration of the "Species Plantarum" of Linnaeus as a Basis for the Starting Point of the Nomenclature of Cryptogams. Professor W. G. FARLOW.

Notes on Some Beaufort Fishes. E. W. GUDGER.

On the Effect of External Conditions on the Reproduction of Daphnia. Dr. J. F. MCCLENDON.

Are Fluctuations Inherited? Dr. HARRY H. LOVE.

Inheritance in Potatoes. Professor EDWARD M. EAST.

Shorter Articles and Correspondence: The Age of Speed Sires: Professor F. R. MARSHALL.

Notes and Literature: Russo on Sex-Determination and Artifical Modification of the Mendelian Ratios, Professor W. E. CASTLE; The Bubonic Plague, Professor H. B. WARD; Desert Plants, WILLIAM L. BRAY.

CONTENTS OF THE AUGUST NUMBER

Chromosomes and Heredity. Professor T. H. MORGAN.

Spiegler's "White Melanin" as Related to Dominant or Recessive White. Dr. ROSS AIKEN GORTNER.

Shorter Articles and Correspondence: A Pickwickian Contribution to Our Knowledge of Wasps: Professor KARL PEARSON.

Notes and Literature: Heredity, Dr. W. J. SPILLMAN.

CONTENTS OF THE SEPTEMBER NUMBER

Nuclear Phenomena of Sexual Reproduction in the Algæ. DR. BRADLEY MOORE DAVIS.

Nuclear Phenomena of Sexual Reproduction in Fungi. PROFESSOR R. A. HARPER.

The Pose of the Sauropodous Dinosaurs. DR. W. D. MATTHEW.

Shorter Articles and Discussion: Evolution without Isolation, DR. JOHN T. GULICK. Retroactive Selection, CASPER L. REDFIELD. The Logic of Chance in Problems of Genetics, ARTHUR S. DEWING.

Notes and Literature: Animal Structure and Habits, Professor G. H. PARKER. Plant Physiology, C. L. SHEAR.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

VOL. XLIV, NO. 527 NOVEMBER, 1910

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with
Special Reference to the Factors of Evolution

CONTENTS

Page

I. **Heredity of Skin Pigmentation in Man.** GERTRUDE C. DAVENPORT and CHARLES B. DAVENPORT - - - - - - - - - - - - 641

II. **The Color Sense of the Honey Bee--Can Bees distinguish Colors?** JOHN LOVELL - - - - - - - - - - - - - 673

III. **Shorter Articles and Discussion:** The Arithmetic of the Product Moment Method of Calculating the Coefficient of Correlation: Dr. J. ARTHUR HARRIS - - 693

IV. **Notes and Literature:** Schlosser on Fayûm Mammals, Dr. W. D. MATTHEW The Ophidian Genus Grayia: Professor T. D. A. COCKERELL - - - - 700

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

THE BULLETIN—For bargains in Ethnolographical and Pre-historic Specimens. Books on Natural History, Science, Travel, Voyages, etc. See THE BULLETIN post free for 3 cent stamp.

4 Duke St., Adelphi—London—England

NATURE

BOOKS

FRANKLIN BOOKSHOP

S. N. RHOADS, Prop.

920 Walnut St. Philadelphia

Second-hand Books Relating to Natural History.

Write for New Catalog.

Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

Henry Holt & Company

34 West 33d St., New York

378 Wabash Ave., Chicago

Microscopes and Accessories

Hand Cameras of Highest Quality

Binoculars, Prism and Galilean

the best obtainable for Nature Study

Scientific Instruments

Laboratory Apparatus

Max Meyer 18 West 27th St. New York

"Quality, Prices, Service Right."

THE

AMERICAN NATURALIST

VOL. XLIV November, 1910 No. 527

HEREDITY OF SKIN PIGMENTATION IN MAN

GERTRUDE C. DAVENPORT AND CHARLES B. DAVENPORT

CARNEGIE INSTITUTION OF WASHINGTON, STATION FOR EXPERIMENTAL EVOLUTION, COLD SPRING HARBOR, N. Y.

A. Introduction ....
B. Anatomical Relations and Kinds of Skin Pigment..........
C. Heredity of Skin Pigment in Typical Caucasians..........
    (*a*) Blond × Blond (Table I) ....
    (*b*) Brunet × Blond (Table II) ....
    (*c*) Brunet × Brunet (Table III) ....
    (*d*) Intermediate × Intermediate (Table IV) ....
    (*e*) Intermediate × Blond (Table V) ....
    (*f*) Intermediate × Brunet (Table VI) ....
    (*g*) Comparisons and Conclusions (Tables VII, VIII)..........
D. Heredity of Skin Pigmentation in Crosses between Whites and Negroes ....
E. Inheritance of Albinism ....
    I. Both Parents are Albinos (Cases 1–3)..........
    II. Neither Parent Albinic ....
        (*a*) Albinos in Caucasian Families with Admitted Consanguinity (Cases 4–6) ....
        (*b*) Albinos in Families with Suspected Consanguinity (Case 7) ....
        (*c*) Albinos in Caucasian Families with no Evidence of Consanguinity (Cases 8–23) ....
        (*d*) Colored Families (Cases 24, 25) ....
    III. One Parent Albinic (Cases 30, 31) ....
    IV. The D.G.V. Family ....
    V. The Condition of Hair and Eye Color in the Pigmented Parents of Albinos (Tables IX, X, XI) ....
    VI. The Origin and ''Cause'' of Albinism (Tables XII, XIII)
    VII. Conclusions ....
F. Literature Cited ....

A. INTRODUCTION

In the modern discussions on heredity there are those who, without undertaking experiments themselves, assume an attitude of hostility to the work of the experimental investigators of heredity and have taken a last stand in the phenomena of inheritance of human skin color. Pearson (1909), who has urged that the collection of extensive statistics is a prerequisite of deductions in the field of heredity, has actually published the non-quantitative impressions of a medical correspondent in the West Indies concerning the method of inheritance of skin color in negro × white crosses and concludes that "in view of the opinion" cited "the suggestion that skin color 'mendelizes' should not be vaguely made." He thinks his correspondent's "views" establish "the main point" "that the segregation in the second generation to pure white or black skins does not occur." On the other hand, a writer in the *Mendel Journal,* No. 1, has also a correspondent in the zone of intermingling whose observations indicate partial, if not complete, segregation. Altogether the subject seems to deserve a more extended, less biased treatment.

B. ANATOMICAL RELATIONS AND KINDS OF SKIN PIGMENT

The pigment of the skin, at least the melanic pigment which alone concerns us here, has its basis in the fine granules lying in the deeper layers of the stratum mucosum of the skin. The granules themselves are of mesodermal origin and the pigment cells—melanoblasts—seem to penetrate from below into the mucosa. Ehrmann (1896, Taf. XI, Fig. 24; Taf. IX, Fig. 19) has figured these melanoblasts in sections of the skin, both of brunets and of negroes. They are much the more abundant in negroes. The anatomical facts are that black skin pigment is made up of many discontinuous elements—the pigment granules. But the mosaic is so fine that, to the naked eye, the color is apparently uniform and a unit. The anatomical differences between the skin of a brunet and a blond suggest that the grades of color may be due to more or fewer of the elements of the mosaic, and that would seem to be a discontinuous variation; but, on the other hand, since these granules increase in size and number during melanogenesis the difference in skin color between a negro, a mulatto, a brunet and a blond may be merely a difference in the point at which the essential melanogenetic process is stopped.

Besides the melanic pigment a yellow-red pigment is often present in skins of all races. This pigment is commonly considered a lipochrome and, in hair at least, is quite different in structure from melanic pigment.

C. HEREDITY OF SKIN PIGMENT IN TYPICAL CAUCASIANS

The data for the study of inheritance in ordinary skin pigment of whites were obtained from two sets of inquiries. The first set was supplied chiefly by school children on cards 127 mm. by 203 mm., which called also for data on the form and color of hair and the color of eyes. The second set was derived from the Family Records filled out for over 300 families, largely by adult persons, including many men in professional life, genealogists and students, as well as farmers and men of affairs.

The directions as to use of terms were necessarily brief. In the first set they ran as follows: "4. Natural complexion or skin color. Use terms as follows: blond, brunet, intermediate, yellowish-white, olive-yellow, dark yellow-brown (dark olive), copper colored, chocolate, sooty black, full black, three fourths black, one half black, one fourth black." I willingly grant that terms are poor means of expressing degrees and quality of skin pigment. Nevertheless, blond and brunet are understood widely in the same sense and it was hoped that "intermediate" would be freely used in doubtful cases. This expectation was not fully justified, since of 1,275 offspring recorded only 513, or 40 per cent. of all, were recorded as of "intermediate" color, while 460, or 36 per cent., were given as blond and 302, or 24 per cent., as brunet. In the "Family Records" the nomenclature suggested was: "Complexion or skin color: *f* (fair), *i* (intermediate), *br* (brunet), *d.br* (dark brown)," etc. The returns in the family records are for 1,098 children, of whom 326, or about 29.5 per cent., are given as of "intermediate" color; 635, or 58 per cent., as fair, and 137, or about 12.5 per cent., as brunet. Evidently "blond" is used in a more restricted sense than "fair" by the population who filled out the blanks in question. All records together are of 2,394 children. Of these there are 843 intermediates, or 35.2 per cent., 1,129 "blond" or "fair," or 47.2 per cent.; and 422 "brunet," or 17.6 per cent. We thus see that only a little over one third of the children are recorded as having an intermediate skin color, while to nearly half are assigned the term "blond" or "fair." The "brunets" are a relatively small proportion of all children in the families under consideration. "Blond" and "fair" have certainly been used too broadly and this must affect somewhat the clearness of our results. However, taking the returns as they come, we shall be able to deduce certain conclusions of importance.

In the following tables we have entered the grandparental data as given. We have, however, not used in the statistics the grandparents as parents, not only because in that case only a single child of the family is known, but especially, because the order of accuracy of the grandparental data is, on the whole, inferior to that of the parents and children. By and large, the grandparental data are highly suggestive, but exceptional cases must be lightly weighted.

(*a*) *Blond* × *Blond* (Tables Ia, Ib).—From two "blond" or "fair" parents 526 children were altogether recorded, of which 472, or 89.7 per cent., were "blond," 40, or 7.6 per cent., were "intermediate," and 14, or 2.7 per cent., were "brunet." Owing to the fact that the number of brunets given is very small and because it

TABLE IA

COMPLEXION: BLOND × BLOND

Family Name.	Children.			M.	F.	MM.	MF.	FM.	FF.
	Blond.	Inter.	Brun.						
Bry.	3		1	bl	bl	bl	br	bl	bl
Bug.	2			bl	bl	bl	bl	i	bl
Cal.	4			bl	bl	—	—	—	—
Cap.	1	1		bl	bl	i	i	i	i
Car.	3	2		bl	bl	bl	—	br	—
Cla.	1			bl	bl	bl	bl	i	bl
Deg.	2			bl	bl	—	i	br	bl
Edw.	2	1		bl	bl	—	—	—	—
Eli.	1			bl	bl	br	bl	br	bl
Fay.	2			bl	bl	bl	bl	br	bl
Fir.	4			bl	bl	i	bl	bl	i
Fou.	1			bl	bl	i	i	bl	i
Fue.	3			bl	bl	bl	bl	bl	bl
Gra.	1	1		bl	bl	bl	i	i	bl
Hal.—A	2	2		bl	bl	br	i	bl	bl
Hed.—D	6			bl	bl	bl	bl	bl	bl
How.—C	6	1		bl	bl	bl	bl	bl	bl
Ker.	3	1		bl	bl	bl	bl	i	bl
Klo.	4			bl	bl	bl	bl	—	bl
Koo.	1		1	bl	bl	bl	bl	bl	bl
Kra.	3			bl	bl	bl	bl	bl	bl
Lav.	3			bl	bl	bl	bl	bl	bl
Len.	6			bl	bl	br	br	br	br
Lit.—B.	3			bl	bl	bl	bl	bl	i
McC.	2			bl	bl	bl	—	bl	bl
McG.	7		1	bl	bl	bl	bl	bl	bl
Mye.	4			bl	bl	bl	bl	bl	bl
Pad.	5			bl	bl	i	bl	—	—
Pla.	6			bl	bl	bl	bl	bl	bl
Reg.	6			bl	bl	bl	i	bl	bl
Sha.	6			bl	bl	bl	bl	i	bl
Sim.	3		1	bl	bl	bl	bl	bl	—
Ste.—F	2			bl	bl	bl	bl	bl	bl
Ste.—G	1	1		bl	bl	br	bl	br	—
Sto.—D	2			bl	bl	bl	bl	i	br
Sto.—E	3			bl	bl	i	i	i	i
Str.—A	5			bl	bl	i	bl	bl	i
Str.—E	2			bl	bl	bl	bl	bl	i
Totals (135)	121	10	4						

38 families.

seemed likely that the rule established for hair color would hold here (namely, that two light parents have no dark children), I asked for further details from all families returning dark children of two blond parents. Only two replies were received. In the case of a family returning two brunets and four blonds from two blond parents the new record gave the father as brunet instead of blond. In the case of the second family said to con-

TABLE Ib

Complexion: Fair × Fair

Family Name.	Children.			M.	F.	MM.	MF.	FM	FF.
	Fair.	Inter.	Brun.						
Bar—4	4			f	f	f	f	f	f
Bel.—1	2	2		f	f	f	f	f	br
Bet.—1	6	1		f	f	—	f	i	f
Bio.—1	6			f	f	f	f	f	f
Bli.—1	6			f	f	f	f	f	f
Bra.—3	7			f	f	f?	f	f	dk
Bre.—2	3			f	f	f	f	f	f
Bro.—2	3			f	f	—	i	—	—
Bro.—8	3			f	f	—	—	—	—
Bro.—10	5	1		f	f	i	f	f	f
Bur.—1	4			f	f	f	f	f	f
Bus.—1	5			f	f	—	—	—	—
Che.—1	2			f	f	f	f	f	f
Coc.—1	2	3		f	f	f	f	f	f
Cog.—2	4		1	f	f	f	i	f	f
Com.	4			f	f	i	—	i	—
Con.	6			f	f	f	f	i	f
Cro.—1	5			f	f	f	f	f	f
Dol.—2	4			f	f	f	f	br	f
Elk.—1	4			f	f	f	f	br	f
Gie.	6			f	f	—	—	—	—
God.	5			f	f	br	f	f	i
Goo.	5			f	f	br	i	f	f
Had.—2	2	1		f	f	f	f	f	i
Hit.	4			f	f	f	f	f	f
Hit.	4	1		f	f	f	f	f	f
How.—1	6			f	f	f	f	f	f
How.—2	2			f	f	f	i	i	i
Jac.—2	3			f	f	f	f	f	f
Joh.—1	5	1		f	f	f	f	f	br
Jon.—2	2	1		f	f	f	i	br	f
Key.—1	4			f	f	f	f	f	f
Kir.—1	11			f	f	f	f	f	f
Klo.	4			f	f	f	f	—	f
Kor.	4	1		f	f	f	—	—	—
Kra.	3			f	f	i	f	f	f
Lan.	3			f	f	—	i	i	f
Lar.	9			f	f	f	f	f	f
Len.	6			f	f	br	i	f	f
Lit.	7			f	f	f	f	f	f
Mar.	5			f	f	f	f	f	f
Mar.	2			f	f	f	br	br	f
McC	10			f	f	f	f	f	f
Mey.—3	3			f	f	br	f	f	f
Obi.	10			f	f	f	f	f	f
Ord.—1	3			f	f	i	f	i	f
Par.	2			f	f	f	br	f	br
Pec.	3			f	f	f	f	f	f
Per.	4			f	f	f	i	f	i
Pic.—1	1	1		f	f	f	i	br	f
Ran.	2		1	f	f	—	—	f	br
Ran	2	1	1	f	f	br	f	f	f
Rec.	3	1		f	f	br	f	—	—
Rid.	3			f	f	—	br	i	f
Roe	3	1		f	f	f	f	f	i

Family Name.	Children.			M.	F.	MM.	MF.	FM.	FF.
	Fair.	Inter.	Brun.						
Row.	8			f	f	i	i	f	f
Rud.	9			f	f	br	f	f	f
Sch.	10			f	f	f	f	f	f
Sco.—2	6			f	f	br	f	f	f
She.—2	3			f	f	f	f	f	f
Shi.—1	2			f	f	f	i	f	i
Sim.	4			f	f	br	f	f	f
Smi.—1	2	1		f	f	i	i	—	i
Spa.	2	4	1	f	f	br	f	f	—
Str.—2	4	2		f	f	i	f	f	i
Sve.	6			f	f	br	f	f	f
Tau.—2	3	1		f	f	f	—	i	i
Tud.—1	3			f	f	f	f	f	f
Vel.	9	1		f	f	f	f	i	f
Ver.	5			f	f	f	f	f	f
Wan.	3			f	f	i	f	f	i
War.—1	3		1	f	f	br	f	br	br
Wes.	4			f	f	br	f	f	f
Wha.—1	9			f	f	f	f	f	f
Whi.—1	3			f	f	f	f	f	f
Win.	7			f	f	f	f	—	—
Wof.	7			f	f	f	f	f	f
Totals (378)	348	25	5						

77 families.

sist of two blond, one intermediate and one brunet offspring, the new record gave the mother as intermediate instead of blond, and the brunet child as light brunet or intermediate, but somewhat darker than the mother. These two families and a third (which is inaccessible) comprising five blonds and four brunets, were therefore struck out from the blond × blond table, leaving only four brunets, or about 3 per cent., among the 135 offspring, recorded in Table IA. Tables IA and IB give 9 brunets among 513 children, or 1.75 per cent. Keeping in mind the probability of occasional blunders on the part of the recorders, it seems doubtful if these nine cases are properly included. The conclusion seems justified that *when both parents have blond complexion or fair skin all of their children will have a similar fair skin.*

(*b*) *Brunet* × *Blond* (*fair*) (Table II).—The offspring of dark by light skin color is of importance because it should throw additional light on the question of dominance, if any. The families of two such parents are

TABLE II

Complexion: Blond × Brunet

Family Name.	Blond.	Inter.	Brun.	M.	F.	MM.	MF.	FM.	FF.	Blond	Inter.	Brun.
And.	10			br	bl	br	lt. blo	bl	bl			
Bex.—1	2		2	br	f	f	f	f	i			
Bin.—1	1	1	1	f	br	br	f	br	br			
Boh.—2	2		1	br	f	f	f	br	i			
Boy.—1	4	2	1	f	br	br	f	f	f			
Bra.—3	5		3	br	bl	br	br	br	br			
Bro.—C	3	1	3	br	bl	br	br	br	i			
Bro.—5	3	2		br	f	—	—	—	—			
Bul.				br	bl	bl	br	bl	bl		2	
Bur.—2	3	1		f	br	f	f	br	br			
Byn.—1	1		1	br	f	br	f	f	f			
Car.—B				br	bl	br	i	bl	i		1	4
Car.—1	2	2		br	f	i	br	f	f			
Cas.	2			br	bl	bl	br	bl	br			
Cla.—1				br	f	br	i	f	i		2	
Clo.	1			bl	br	i	i	br	br			
Cor.	4	2	2	br	f	br	i	f	f			
Coz.	4	1		br	bl	i	br	br	br			
Cro.	3			br	bl	i	i	i	bl			
Cur.				br	bl	bl	br	bl	i			4
Cuw.	1	1	1	bl	br	i	bl	br	br			
Dig.—A	2	2	1	br	bl	—	—	—	—			
Doo.				bl	br	i	br	br	bl		1	4
Dra.	1	1		br	bl	br	i	i	i			
Dye.	2	2	1	bl	br	bl	i	br	br			
Edw.	3		2	br	f	i	f	f	f			
Edw.	4	2	2	f	br	f	i	y	br			
Eld.	3		1	f	br	f	f	br	br			
Eve.	4		1	f	br	f	f	f	i			
Fal.	5	1	1	bl	br	bl	bl	bl	bl			
Gla.	1		2	br	f	br	br	f	f			
Gla.—B	3	1	3	br	bl	bl	br	bl	i			
Goe.	1	1		f	br	br	br	br	br			
Gre.—E	1		2	bl	br	br	br	br	br			
Gri.	5	1	1	br	bl	bl	i	bl	br			
Hag.				br	f	f	br	—	—		4	
Hal.—E				br	bl	br	br	bl	bl			5
Han.—1				br	f	br	br	f	f			2
Har.—D	1		1	bl	br	bl	br	br	br			
Hof.	4	1		bl	br	bl	br	br	br			
Hom.—B	4		2	bl	br	bl	bl	—	—			
Hur.	2		2	br	f	br	f	f	f			
Hyd.—1	4	1	1	br	f	f	br	f	br			
Jal.	1		4	br	f	f	br	f	f			
Jem.				br	bl	bl	br	br	bl		2	1
Jen.	1	2	2	br	f	i	br	f	—			
Jon.—B	3		3	bl	br	bl	bl	br	bl			
Jon.—1	2	1		d.br	f	i	i	br	f			
Jon.—3				f	d.br	f	f	br	br		3	1
Koc.—1	1	3	8	br	f	br	i	f	f			
Koc.—2				bl	br	bl	i	i	br		4	1
Lot.—A	3		2	br	bl	br	br	br	br			
Lym.—1				br	bl	br	br	br	bl			3
Lym.—2	3			f	br	i	f	i	i			
Mai	4	3	1	f	br	i	f	br	f			

Family Name.	Blond.	Inter.	Brun.	M.	F.	MM.	MF.	FM.	FF.	Blond.	Inter.	Brun.
Mat.	2			bl	br	br	br	bl	br			
McC.	5			br	f	br	br	f	br			
Mil.	3	2		br	bl	bl	—	bl	i			
Mil.—B	2		4	bl	br	bl	bl	br	br			
Moo.				br	bl	i	br	i	i			2
Owe.—1				br	f	f	br	—	—		2	
Par.	2	2	2	f	br	i	f	f	br			
Pat.				br	bl	br	i	br	br		1	3
Pre.	3	2	1	br	bl	i	br	bl	br			
Red.	2			br	bl	br	i	bl	bl			
Rei.—1	2	2	2	br	f	i	f	d.br	f			
Rel.	1		2	br	bl	—	—	—	—			
Ril.	3	1	2	bl	br	i	bl	i	i			
Sca.	3		1	bl	br	bl	bl	bl	br			
Smi.—E				br	bl	bl	—	—	—		4	
Spr.	2		2	bl	br	—	—	—	dark			
Ste.—C	2		3	bl	br	i	bl	br	i			
Ste.—2	2			br	f	f	f	f	f			
Str.—D	2			bl	br	i	br	br	bl			
Syk.	6	1	1	bl	br	—	—	br	br			
Tat.	5		1	br	bl	br	br	bl	bl			
Van.—1				br	f	f	br	f	i		2	1
Ven.—1	4	1		f	br	i	i	br	br			
Vos.	1	2		bl	br	i	i	br	br			
War.—A	1		1	br	bl	br	i	i	i			
Wen.	4	2	2	br	f	f	—	i	f			
Whi.				f	v.br	f	v.br	f	v.br		2	
Whi.	2	4	4	f	br	f	f	br	f			
Whi.—3	3	2	2	f	br	f	i	f	br			
Wil.	2		2	bl	br	i	bl	br	br			
Wol.	2	1	1	f	br	f	d.br	i	f			
Wor.	3	1		bl	br	bl	br	—	—			
Wyb.	4			br	f	i	i	f	f			
Total (342)	193	58	91						(60)	0	30	31

Total: 88 families. 70 families. *v.br*, very brown. 18 families.

given in Table II, and are divided into two classes, viz., those containing blond offspring, on the left side of the table, and those containing none, on the right side. The division is made in accordance with the hypothesis that "brunet" is dominant to "blond" and that the brunets may be of two sorts, either duplex or simplex. in respect to the pigmentation character. If the pigmentation factor of the dark parent is duplex no blonds are to be expected, but if the dark parent is simplex in pigmentation half of the children will have little or no black skin-pigment. By hypothesis the simplex parents should be about twice as numerous as the duplex. In Table II there are 70 families with blond children to 18 without blonds. Some of the latter are doubtless without blonds *by chance,* owing to the small number in the family, just as there are 30 families in the entire 88 without brunet offspring or 39 without intermediates. That *all* of the families without blonds are not so by chance is probable from the following considerations: (*a*) blonds are almost (11:12.8) as numerous as the other two classes together yet the latter are *both* absent in the offspring of only eleven families; (*b*) there are more large families that are blondless than that are without brunets and intermediates, and when a large family is without offspring of a particular class the result is less probably due to chance. Finally, owing to the fact that the development of potential pigment is frequently retarded, some of the families with "blond" offspring would later be without blonds. We may conclude, then, that some of the blondless fraternities are so because all of their members have the determiner for skin pigmentation and, consequently, in the brunet × blond matings some of the brunet parents are duplex in skin pigment. But the offspring of these duplex parents are not all alike; half of them are "intermediate" and the remainder "brunet." This result suggests that brunets may carry the "intermediate" grade of skin pigmentation as a hidden—hypostatic—factor.

In the families containing blond offspring, expectation, on the hypothesis of segregation, is that half of the offspring shall be blond and half pigmented in full or intermediate grade. Actually blonds are to non-blonds as 193:149 or as 1.3:1. The excess of blonds suggests that some of them are immature and potentially pigmented, the families really belonging to the right hand side of the table.

(*c*) *Brunet × Brunet* (Table III).—When both parents are brunets there may, on the segregation theory, be two classes of families, namely, a class in which both parents produce germ-cells without the pigment determiner and a class in which at least one parent produces no such germ-cells. In the former case only are blond

TABLE III

COMPLEXION: BRUNET × BRUNET

Family Name.	Blond.	Inter.	Brun.	M.	F.	MM.	MF.	FM.	FF.	Blond.	Inter.	Brun.
Ait.—1	3		1	br	br	f	br	f	f			
Alt.	1		4	br	br	bl	bl	br	—			
Arn.—2				br	br	br	i	br	i		2	1
Bal.—3	1		4	br	br	f	br	i	br			
Ban.	1	1	1	br	br	i	br	br	br			
Bay.				br	br	br	i	br	br		1	4
Blo.—1				br	br	—	br	br	—		3	2
Bro.—B	2		1	br	br	br	br	br	i			
Bu.	1		1	br	br	br	bl	—	br			
Can.				br	br	br	br	br	bl		2	
Cla.—D	2	1	4	br	br	br	br	lt	lt			
Col.—D	2		2	br	br	i	br	i	br			
Eni.				br	br	i	br	br	br			3
Fie.	3	1	1	br	br	i	br	br	i			
Fis.				br	br	br	br	i	—			3
Gim.	1		2	dk	dk	f	dk	dk	dk			
Gre.—C	1		4	br	br	br	—	i	—			
Hen.				br	br	br	br	br	br			3
Hen.				br	br	br	i	br	—		1	5
Jac.—1	2		1	br	br	br	f	i	f			
Jor.—2	1	1	1	br	br	—	—	br	br			
Kay.				br	br	br	br	i	br		2	2
Kel.	4		3	br	br	br	f	br	f			
Kil.	2	1		br	br	i	—	—	—			
Kub.				br	br	br	br	bl	br		1	2
Lan.	1	2		br?	br?	bl	bl	bl	bl			
Lan.	2		2	br	br	br	br	br	br			
McB.				br	br	br	br	br	br			5
McC.	2		1	br	br	bl	br	—	—			
Mel.	2		3	br	br	i	f	br	br			
Mor.—A				br	br	i	i	br	br			2
Par.—B				dk	dk	i	br	br	br		1	2
Pib.—1				br	br	br	br	br	br			7
Pil.—2				br	br	br	br	i	br			5
Pon.	2	1		br	br	br	bl	br	—			
Ram.				br	br	br	br	br	br			3
Rob.—B				br	br	i	i	br	br		1	3
Sin.—D				br	br	br	br	br	br		3	1
Was.				br	br	i	br	i	br		2	3
Wri.	3	2	2	br	br	br	br	bl	i			
Wro.—B				br	br	br	bl	br	bl			2
You.	2	1	1	br	br	bl	i	bl	br			
Zin.	1		4	br	br	—	bl	—	—			
Total (96)	42	11	43						(77)	0	19	58

Total: 43 families. 23 families. 20 families.

offspring to be expected. Among the 43 families of Table III, 20 produced no blonds, although some of them comprise four to seven children. Consequently it is highly probable that some brunets are duplex in skin pigmentation. In the families that produce blonds there are only 54 children out of a total of 96 that are either brunet or intermediate, or about 56 per cent. of all. With simple segregation and dominance 75 per cent. of dark offspring are to be expected; the deficiency is, I suspect, partly due to the exclusion from the left side of the table of some families with both parents simplex merely because they failed (in their small families) to produce blonds, although they were *potential* blond producers.

(*d*) *Intermediate* × *Intermediate* (Table IV).—The intermediate class serves to include those whose skin has not the clear, transparent, pink quality of the typical blond, on the one hand, nor the rich dark shade of the brunet. It was intended to include a considerable range of color from 10 per cent. to 18 per cent. of black in the color wheel. As already stated, however, collaborators assigned less than a third of the offspring to this class.

The distribution of skin color in the offspring of two intermediates offers, it must be freely admitted, great difficulties. There are several possibilities. It might be that the "brunet" type of skin color is typical for skin pigment. Accordingly, the intermediate condition may be conceived as having been stopped part way in color development. This stoppage may be due to the fact that the units essential to the later phases of color development are lacking, or to the fact that the stimulus to full pigmentation is weak. The first alternative assumes many units for pigmentation; the second, one unit that fluctuates widely. Again the intermediate condition might be the consequence merely of its simplex or heterozygous nature. If the latter were the case two intermediates should produce light and dark offspring again in nearly equal proportions as well as intermediates. But if either of the two first-named hypotheses is correct, in accordance with results found by us in hair color, the offspring should not exceed in pigmentation the more pigmented parent; in the same way that in the offspring of two blond parents the parental color is not exceeded.

Table IV gives the data precisely as reported. As in

TABLE IV

INTERMEDIATE × INTERMEDIATE

Family Name.	Children.			M.	F.	MM.	MF.	FM.	FF.
	Fair.	Inter.	Brun.						
Ave.—1		5		i	i	br	i	i	i
Bal.—A		6		i	i	i	i	i	i
Bal.—B	1	1		i	i	i	i	—	—
Bar.—2	3	4	2	i	i	i	f	i	f
Bar.—A	2	4		i	i	f	i	i	f
Bar.—3	2	2		i	i	i	f	i	i
Bat.—B	1		2	i	i	i	br	i	br
Bec.		5		i	i	i	i	br	i
Bec.—B		2		i	i	i	i	i	—
Bed.		2		i	i	i	i	i	i
Bre.—1		2		i	i	i	i	i	i
Bel.—1	1	1	2	i	i	br	f	br	i
Ber.	2	3		i	i	i	i	i	i
Bis.	3	3	1	i	i	i	br	i	i
Bla.	2	2	1	i	i	i	bl	bl	i
Bra.—4	3			i	i	i	br	i	br
Bra.—D	1	4	1	i	i	bl	i	i	i
Bro.—9		3		i	i	f	i	i	—
Bur.	2	2		i	i	br	i	i	i
Bur.—3		3		i	i	i	i	—	—
Cad.—2		5		i	i	?	f	i	i
Cal.—1		3		i	i	i	br	i	i
Cap.	2	2		i	i	i	i	bl	—
Cas.	1	9		i	i	i	br	i	i
Cha.		2	1	i	i	i	i	i	br
Cla.—2	1	3		i	i	i	i	i	i
Col.		4		i	i	i	i	—	—
Con.		5		i	i	i	i	i	i
Con.	1	1	1	i	i	br	bl	br	i
Con.—D		3		i	i	i	i	i	i
Con.—E		2	2	i	i	i	i	br	bl
Cox.	1	4		i	i	i	i	—	—
Dar.—B		2		i	i	i	i	br	i
Dar.—D		4		i	i	i	i	i	i
Dav.—1		2		i	i	i	i	br	i
Dav.—E	1	6		i	i	i	i	i	i
Dol.—1		13		i	i	i	i	i	i
Don.—1		8		i	i	i	i	i	br
Ear.	1	1		i	i	i	bl	i	bl
Eck.—1	3	1	2	i	i	i	f	f	i
Fer.		2		i	i	—	—	—	—
Gan.		2		i	i	i	bl	br	i
Gar.	1	4	2	i	i	i	i	i	i
Gen.	2	2		i	i	—	—	—	—
Goo.—2	2	1		i	i	br	f	f	i
Gra.—A	2	2		i	i	br	i	bl	br
Gro.—A		3		i	i	i	—	i	—
Gue.	6	2	2	i	i	i	i	i	br
Had.—B		3		i	i	dk	bl	i	br
Hal.	1	1		i	i	i	bl	i	i
Har.—A	4	3	3	i	i	bl	bl	bl	br
Har.—1		3		i	i	i	i	i	i
Har.—2	1	7		i	i	i	i	i	i
Haw.		3		i	i	—	—	i	i
Hay.	1	2	1	i	i	br	i	br	i

Family Name.	Children.			M.	F.	MM.	MF.	FM.	FF.
	Fair.	Inter.	Brun.						
Hil.	1	1		i	i	i	i	i	i
Hog.—B	1	1	1	i	i	bl	br	—	—
Hoh.		6		i	i	i	i	i	i
Hol.	2	3		i	i	f	—	f	i
Hoy.		4		i	i	i	i	i	i
Hub.		4		i	i	i	i	i	i
Huf.	1	2		i	i	i	i	i	i
Irw.		2		i	i	i	i	i	i
Jam.	1	1	1	i	i	br	i	f	i
Keh.		2	3	i	i	i	br	br	i
Kei.		3		i	i	i	f	i	f
Kun.		1	1	i	i	i	i	i	br
Lay.		5		i	i	i	i	i	i
Lea.		3		i	i	i	i	i	i
Lit.—C	4		2	i	i	i	bl	i	i
Loc.—A	2	2	1	i	i	i	i	i	i
Loc.—B	1	1		i	i	bl	i	i	i
Loe.		4		i	i	bl	br	bl	bl
Loh.		3	2	i	i	—	—	—	—
Los.		4		i	i	i	br	i	i
Lum.	1	5		i	i	i	i	i	i
Mac.	2	1		i	i	bl	i	br	i
Mag.		5		i	i	i	i	i	i
Mar.—B		3		i	i	i	i	i	i
Max.		2		i	i	i	i	i	i
McC.—2			2	i	i	br	i	i	i
McD.	1	3		i	i	bl	i	i	i
McM.	3	3		i	i	i	i	i	i
Mea.		2	2	i	i	i	br	i	i
Mel.	1	5		i	i	i	br	br	i
Mer.		4		i	i	i	i	f	i
Mil—G	3	1		i	i	i	i	i	i
Mit.—C.		2		i	i	i	br	i	br
New.	1	5	1	i	i	i	i	i	i
New.	1	3	1	i	i	br	i	i	i
Nic.—2		3		i	i	f	br	i	i
Nor.	4	1		i	i	i	i	i	bl
Nur.		4		i	i	i	i	i	i
Pal.		1	1	i	i	br	bl	i	br
Pat.—A.	2	8		i	i	i	i	i	i
Pla.		2	1	i	i	i	i	—	i
Ran.—B		9		i	i	i	i	i	i
Rau.	1	1		i	i	bl	i	i	bl
Ree.		9		i	i	i	f	olive	i
Rem.	1	1		i	i	i	i	i	i
Ric.—C	2	1	2	i	i	br	i	br	br
Rin.	2	1	1	i	i	f	f	br	i
Rit.	1	3		i	i	i	i	i	i
Rob.	1	1	3	i	i	i	br	br	i
Rog.		4		i	i	i	i	br	i
Ros.		5		i	i	i	i	i	i
Rud.		3		i	i	i	i	i	i
Rus.	2	4		i	i	—	—	—	—
Sam.—C	2	2	1	i	i	i	i	i	i
Sam.—B	1	4		i	i	i	i	i	i

Family Name.	Children.			M.	F.	MM.	MF.	FM.	FF.
	Fair.	Inter.	Brun.						
Sam.—A	1		1	i	i	i	br	bl	br
Say.		2		i	i	i	i	i	br
Sea.	1	1		i	i	f	i	i	i
Sil.—B		3		i	i	br	i	i	br
Sil.—C		2	1	i	i	i	i	bl	i
Sin.		2		i	i	i	i	i	i
Smi.—3	4			i	i	i	i	i	i
Sml.		3		i	i	i	i	i	i
Sne.		2		i	i	i	i	i	br
Sob.	1	2		i	i	br	bl	bl	i
Squ.		5		i	i	i	i	br	i
Ste.—1		2	2	i	i	i	i	br	br
Sti.—1	2			i	i	i	i	i	i
Sto.—C		1	1	i	i	i	i	i	i
Str.—C.	2			i	i	br	i	bl	i
Str.	2			i	i	i	bl	i	bl
Str.		2		i	i	—	—	—	—
Sny.		4		i	i	i	i	i	i
Tay.—D		3		i	i	i	i	i	i
Tho.	2	2		i	i	bl	br	br	i
Tre.		4		i	i	i	i	i	i
Tru.	2	2		i	i	i	bl	i	i
Wal.	4	1		i	i	i	i	i	i
Wal.—2		7		i	i	i	i	i	i
Wan.		3		i	i	i	i	i	i
Wan.—B	1		1	i	i	—	i	i	i
War.—C.		2		i	i	f	f	dk	dk
Wes.	2	1		i	i	br	bl	bl	i
Whe.—D	1	1		i	i	bl	i	i	i
Wil.		3		i	i	i	bl	br	i
Wil.	1	3	1	i	i	—	—	br	i
Wil.—B	1		2	i	i	i	dk	br	i
Win.	1	2		i	i	i	i	i	i
Wol.	1	1	2	i	i	br	br	bl	i
Totals (591)	128	403	60						

the case of the other tables, a certain allowance has to be made for errors in reporting due to vague and incorrect recollection and to other mental lapses. In such families as Keh., McC.—2 and Rob. the color of one of the parents is probably incorrectly reported. Sometimes the probability of the record can be tested by considering the associated hair color, since there is a fairly high correlation between the two. Thus in the case of the Keh. family both "intermediate" parents have "black" hair, while all but one of the "brunet" children have hair that is recorded as of some shade lighter than black. In the McC.—2 and Rob. families both parents and children have "dark brown" hair, but, in both families, the skin

TABLE V

Intermediate × Blond

Family Name.	Children.			M.	F.	MM.	MF.	FM.	FF.
	Blond.	Inter.	Brun.						
Ave.	4	1		i	bl	i	i	i	bl
Bal.	3	1	1	bl	i	bl	br	—	—
Bar.	2			i	bl	i	br	bl	i
Bon.	4			i	bl	i	i	bl	bl
Bow.	3	2		i	bl	i	i	—	i
Col.—C.	2	3		bl	i	bl	br	i	bl
Dav.—C	2	2		bl	i	—	—	br	i
Dru.	2			i	bl	i	br	br	—
Ege.	2			bl	i	bl	—	bl	—
Ewa.	2			bl	i	i	i	i	i
Fin.	1	1		i	bl	i	br	i	i
Fra.	3	1	2	i	bl	—	—	—	—
Fra.—D	2			i	bl	—	—	—	—
Fri.—B	1	2		i	bl	i	i	i	bl
Gen.	3			bl	i	i	i	i	i
Gil.—B	3	1		i	bl	i	br	bl	i
Gor.—A	2	7	2	bl	i	bl	i	i	i
Gsc.	2		1	i	bl	br	bl	bl	bl
Hal.—B	4			bl	i	br	bl	i	br
Hal.—D	1	1		bl	i	i	bl	i	i
How.—D	3			bl	i	i	bl	i	i
Hur.	1	3		bl	i	i	i	i	i
Kel.	1	1		bl	i	bl	i	i	bl
Kir.	1	1		bl	i	i	i	i	i
Lat.—B.	3			bl	i	bl	i	i	i
Ma.	1	1	1	bl	i	bl	bl	bl	i
Mil.—D	2			bl	i	br	i	br	bl
Mos.	2	3		i	bl	i	i	i	bl
Pie.		2		i	bl	i	i	br	i
Pla.—C		1		i	bl	br	bl	i	bl
Pra.	4	4		bl	i	bl	i	dk	dk
Ras.—B	1	4		i	bl	bl	br	—	—
Rob.	3	4		i	bl	i	i	bl	i
Sco.	3	2	1	bl	i	bl	br	bl	br
Sco.—B	2			bl	i	bl	bl	i	i
Sha.	2			bl	i	i	i	bl	i
Str.	4	2		bl	i	bl	bl	bl	—
Suo.		7		i	bl	br	bl	—	bl
Tw.	3	1		bl	i	bl	bl	—	—
Vos.	2	1		bl	i	br	bl	i	i
Wal.		4		bl	i	i	bl	bl	bl
Web.	6	1		bl	i	bl	br	br	br
Wri.	3			i	bl	fair	i	bl	i
Wro.—C	1	1		i	bl	i	br	bl	bl
Totals: (179)	96	75	8						

44 families.

color of the parents is given as "intermediate," while that of all or most of the children is given as "brunet." It seems probable that in applying the *terms* that were available the difference in skin color between parents and children has been unconsciously exaggerated.

INTERMEDIATE × FAIR

Family Name.	Children.			M.	F.	MM.	MF.	FM.	FF.
	Fair	Inter.	Brun.						
Ba.	4	1	2	f	i	f	i	br	br
Bec.—1	4	2		f	i	f	—	f	i
Beh.	6	1	1	i	f	f	i	i	f
Ben.—3		2		i	f	br	f	f	f
Bet.—2	2		1	i	f	f	br	i	i
Boh.—1	7	2		i	f	—	—	—	—
Bon.	4			i	f	—	i	i	f
Boo.—1	1	3		i	f	f	br	f	i
Boy.	7	2		i	f	f	f	f	f
Bro.—4	3	3		i	f	f	i	f	i
Bye.—1		2		f	i	—	—	i	br
Cah.—1	7	1		i	f	i	f	f	f
Cam.—1	1	3		f	i	i	f	f	br
Can.	5	3		f	i	br	f	br	i
Cha.—3	4	2		f	i	i	f	—	i
Cla.	6	2		f	i	f	f	f	i
Clo.—1	3	5		f	i	f	f	br	i
Coi.—1	1	3		i	f	i	br	f	f
Cra.—1	1	1		i	f	i	i	i	i
Cro.—2	5	2		f	i	i	f	i	i
Cuo.	4			i	f	f	f	f	f
Dar.—1		1	3[1]	f	i[2]	f	i	br	f
Dow.—2	1	2	1	f	i	i	i	br	f
Fox.—1	2			f	i	f	f	i	—
Gar.—1		2		f	i	—	i	i	i
Glo.	6	1	1	i	f	—	—	—	f
Gor.—1	8	1		i	f	—	—	—	—
Has.	3		1	f	i	f	f	—	—
Kas.	3	3		i	f	i	f	—	—
May.	1	2		f	i	i	i	f	i
Mor.—3		1	1	f	i	f	f	f	i
Mun.	1	5	1	f	i	br	f	br	f
Nip	2	1	2	f	i	i	i	i	i
Obi.	4			f	i	br	f	i	i
Ogd.	1	2		f	i	f	f	f	f
Ori.—1	2	2		i	f	i	i	i	f
Owe.—2	5			f	i	f	f	f	f
Ram.	2	2		f	i	i	i	i	f
Rec.	1	3		f	i	—	—	—	f
She.—1	3	3		i	f	i	f	f	i
Sti.—2	1		1	i	f	f	f	i	f
Str.		3		f	i	—	—	i	f
Tit.	4	1		f	i	i	i	i	i
Wal.—1		4	1	f	i	i	i	i	i
Way.	3	1	2	f	i	br	f	f	i
Zop.		3		i	f	f	f	f	f
Total (229)	128	83	18						

46 families.

[1] Medium brown to dark brown hair.

[2] "Black" hair, hazel eyes.

Applying no correction at all, however, practically 90 per cent. of the offspring agree with the rule that they are not darker than their darker parents. Nevertheless, the hypothesis that intermediate skin color is sometimes due to the imperfect dominance of the simplex determiner must be admitted as plausible.

(*e*) *Intermediate × Blond*.—The results of this mating are given in Table V, showing the distribution of skin color in the offspring. If all intermediates were simplex in skin pigmentation we should expect blonds and intermediates in equal numbers. Also on the hypothesis that the higher grade of pigmentation is epistatic we should expect blonds and intermediates, but no brunets. The actual distribution agrees nearly with expectation on either hypothesis: where the term "blond" is used 54 per cent. of the offspring are blonds; and among the "fairs" 56 per cent. are fair. Most of the remainder are "intermediate," the exceptions constituting only about 6 per cent. of all offspring. In some of the most aberrant families, like Dar.—1, one finds in the hair color reason for doubting if classification was always made with judgment. It seems probable that when the parentage really falls into this class brunet offspring rarely, if ever, occur.

(*f*) *Intermediate × Brunet* (Table VI).—If intermediate skin color is simplex then brunet is duplex and expectation is that half of the offspring shall be brunet, half intermediate and there shall be no blonds. But if intermediate and brunet represent two different stages of pigmentation either of which may be epistatic to blond, then a certain proportion (sometimes less than 25 per cent.) of the offspring should be blonds. Actually there are many blonds (about 24 per cent. of all offspring) and consequently the second hypothesis is favored again.

Of the 80 families 39 have no blond offspring; we may inquire if the ancestry of such families differs in the proportions of the blonds from those that produce blond offspring. We find that in the families with blond off-

TABLE VI

Brunet × Intermediate

Family Name.	Blond or Fair.	Inter.	Brun.	M.	F.	MM.	MF.	FM.	FF.
Bea.	3	2	5	br	i	i	bl	bl	i
Bis.—2	1		1	i	br	i	br	i	br
Boh.—3	5	1	3	br	i	—	—	—	—
Boy.—2		1	4	i	br	—	—	bl	—
Bro.—7	2		1	i	br	f	i	br	br
But.		1	2	i	br	br	br	br	br
Clu.—A		3		i	br	—	—	—	—
Clu.—B	1	1	1	i	br	i	—	—	—
Con.	3	2	2	br	i	bl	i	bl	bl
Cur.—A		1	1	br	i	*bl*	*bl*	bl	i
Cur.—1		4	2	i	br	f	i	i	br
Dav.—A.	1	4	2	i	br	—	—	—	—
Dep.		2		i	br	i	—	i	br
Dev.		2		i	br	bl	br	—	bl
Dey.—A	2	1		br	i	br	br	i	br
Don.	1	1	5	br	i	*bl*	*bl*	bl	i
Don.—B.	1		3	i	br	i	bl	bl	br
Dow.—1	5			br	i	f	br	f	f
Dru.—B	2	1		br	i	—	—	—	—
Eas.	2			i	br	br	i	f	br
Fyt.		2	3	i	br	—	—	i	br
Gar.—A	2		3	i	br	br	i	br	i
Gar.—1	2	3	1	br	i	i	br	i	f
Gan.	3	3		br	i	i	i	i	f
Get.		3	2	i	br	i	i	i	i
Gil.		2	2	br	i	br	f	i	f
Gla.—A		6	2	i	br	i	bl	br	br
Gra.—D		3	2	br	i	i	br	i	i
Gre.		2		i	br	br	br	i	i
Had.	2			br	i	i	br	br	i
Han.			2	br	i	bl	br	bl	i
Har.			2	br	i	br	i	i	i
Hay.	1		2	br	i	—	br	br	f
Hen.—A		2	1	i	br	br	i	br	bl
Hew.	3	2	3	br	i	i	—	bl	br
Hir.	1	1		br	i	br	br	i	i
Hit.		2		i	br	i	i	i	br
Hop.		1	1	br	i	i	i	i	br
Jor.—1		2	1	br	i	i	br	i	i
Ker.	1		1	br	i	i	i	i	i
Kro.—1	1	2	1	br	i	br	f	br	i
Leo.		2	1	br	i	bl	br	br	i
Lon.—C		1	2	br	i	br	i	i	i
Lue	1	2	1	br	i	br	br	i	br
McG.	2	1		br	i	i	i	br	i
McK.		2		br	i	f	i	br	i
McL.		2	3	i	br	i	br	br	—
McG.		1	2	br	i	i	i	i	i
Mar.	1	2		br	i	i	f	i	i
Mil.—A.	1	1	1	br	i	i	br	br	i
Mit.—C.		3		i	br	i	br	bl	br
Nic.—A	1	1	3	i	br	i	br	br	bl
Nic.—1		2	3	i	br	i	br	br	i
Oe.		5		i	br	i	i	br	br
Pal	1		1	br	i	f	br	f	br
Poe.		2	1	br	i	br	br	i	i

Family Name.	Blond or Fair.	Inter.	Brun	M.	F.	MM.	MF.	FM.	FF.
Pyn.	1	3	1	i	br	i	br	i	br
Ric.—3	2		2	br	i	f	br	br	i
Roc.	3	2		i	br	i	i	br	br
Rol.		5	1	br	*i*	br	br	i	i
Say.	1		1	br	i	br	i	bl	dk
Sch.	1	2		br	i	br	f	f	f
Sco.—1	2	1		br	i	i	i	i	i
Sel.		1	3	i	br	i	br	i	br
Ser.			2	br	i	br	bl	br	br
Sho.		1	2	br	i	i	bl	br	i
Ski.	2	1	2	i	br	i	br	br	br
Smi.	2	1		br	i	f	i	i	i
Spi.	1	3		br	i	i	f	i	i
Ste.—D		2	5	br	i	br	i	i	—
Sto.—B		1	1	i	br	i	i	br	br
Tho.		3		i	br	i	br	i	*i*
Tre.		2	1	br	i	br	br	i	—
Tuc.	2			br	i	i	bl	bl	br
Tyd.—1		2		i	br	i	i	i	br
Ver.		1	1	br	i	i	bl	i	br
Way.	2	1	1	i	br	—	—	i	i
Web.	1		1	i	br	i	bl	i	i
Wei.	1	1	1	br	i	bl	br	bl	br
Woo.		6	1	i	br	i	br	i	br
Totals (307)	73	129	105						

80 families. Certain grandparental terms are printed in italics to indicate our doubt as to their correctness.

spring 24 per cent. of the known grandparents are recorded as blond or fair, whereas in families without blond offspring only 13 per cent. of the known grandparents are blond or fair. In families with blond offspring 9 of the 34 complete sets of grandparents (or 26.5 per cent.) show blondness on both the paternal and maternal side, whereas in families without blond offspring, of the 36 complete sets of grandparents only 4, or 11 per cent., show blondness on both sides, and the size of the families in these four cases is small, viz., 2, 2, 2, 4, so that there is a large chance that the families are potentially blond producing and really belong in with the blond producing families. It appears, then, that both the intermediate and brunet parents may contain hypostatic blondness, and where they do they will have blond offspring, but not otherwise.

If the brunet parent is, in any case, duplex-brunet and contains no hypostatic intermediate or blond then expectation is that all of its offspring shall be brunet. This condition is apparently not realized even in the 29 families that yield no blonds. Only in seven cases are both [grand] parents of the brown parent "brunet," but there is no evidence that they were not simplex. At any rate, in all these seven cases some "intermediate" offspring were produced.

(*g*) *Comparisons.*—The relations of the foregoing facts are better brought out by the compact table where the results of the various matings can be compared.

TABLE VII

The Number and Distribution of the Offspring of Various Matings

Nature of Mating.	Frequency.				Proportions.		
	Total.	Blond.	Inter.	Brun.	Blond.	Inter.	Brun.
Blond × blond	513	469	35	9	91.4	6.8	1.8
Blond × intermediate	408	224	158	26	54.9	38.7	6.4
Blond × brunet	403	193	88	122	47.9	21.8	30.3
Intermediate × intermediate	591	128	403	60	21.8	68.5	9.7
Intermediate × brunet	307	73	129	105	23.8	42.0	34.2
Brunet × brunet	173	42	30	101	24.3	17.3	58.4
Totals	2,394	1,129	843	423			

Considering alone the proportions of blonds in the families of the various matings, some striking figures are obtained. Three classes appear:

I. Class comprising about 90 per cent. blonds approaching 100 per cent.—blond × blond (91.4 per cent.).

II. Classes in which the blonds constitute approximately 50 per cent.—blond × intermediate (54.9 per cent.), blond × brunet (48 per cent.).

III. Classes in which the blonds constitute approximately 25 per cent.—brunet × brunet (24.3 per cent.), brunet × intermediate (23.8 per cent.), intermediate × intermediate (21.8 per cent.).

In the first class neither parent shows skin pigment; in the second class one parent only shows such pigment; in the third class both parents show skin pigment. The proportions of blonds in the first class are those expected from Mendelian crosses of R × R; of the second class those expected from R × DR crosses, and of the third class those expected from DR × DR matings. Shall it therefore be concluded that all brunets as well as intermediates are simplex in skin pigment? This does not follow; but it does seem to be a fact that duplex "brunet" and "intermediate" are not common;[1] indeed so uncommon as not to alter materially the proportions that would be given on the hypothesis that they are always simplex.

The principle of the non-transgressibility of the upper limit to which we have called attention elsewhere[2] seems to hold for skin pigment also although the result is less clear-cut, probably because the terms were less accurately assigned. To see how closely the law holds Table VIII has been constructed. The three cases: (*a*) darker parent blond; (*b*) darker parent intermediate; (*c*) darker parent brunet—are chosen and the distribution of offspring in each case indicated at the right.

TABLE VIII

SHOWING THE DISTRIBUTION OF THE DIFFERENT CLASSES OF SKIN COLOR IN THE THREE CASES WHEN THE DARKER PARENT IS BLOND, INTERMEDIATE AND BRUNET

Grade of Darker Parent.	Offspring.				Proportions.		
	Frequency.						
	Totals.	Blond.	Inter.	Brun.	Blond.	Inter.	Brun.
Blond	513	469	35	9	91.4	6.8	1.8
Intermediate	996	352	561	83	35.3	56.3	8.3
Brunet	883	308	247	328	34.9	28.0	37.1

Table VIII shows that exceptions to the rule of delimitation are, considering the vagueness of terms,[3] relatively rare, only about 8 per cent., and, consequently, the rule seems verified.

The significance of the intermediate grades of skin color is a question of prime importance. There is some evidence, for example in Table IV, families Har. A, Keh.

---

[1] For examples of probably duplex "brunet" see Table III, Eni, Hen, McB, Ram. Of duplex intermediates there seem to be examples in Table IV, Bal.—A, Dol.—1, Don.—1, Ran.—B, and Ree; and in Table V, Suo.

[2] G. C. and C. B. Davenport, 1909, p. 208.

[3] The proportion would be substantially reduced were returns that show intrinsic evidence of error eliminated.

and Rob., that the intermediate condition is sometimes a simplex or heterozygous condition. But, in most cases the evidence is clear that the "intermediate" grade (or grades) is simply epistatic to blond and hypostatic to brunet and that intermediate may carry, and usually does carry, hypostatic "blond," while brunet may carry, and usually does carry, either or both hypostatic blond or hypostatic intermediate. There is nothing unprecedented in the conception that a given condition may be in some cases simplex and in others act as a unit. Some cases of barring in the plumage color of poultry belong to the one category and others to the other.

The meaning of the case of skin pigmentation, like that of hair pigmentation, is not perfectly clear. There is a possibility that pigmentation stops at certain well-defined points, each of which is determined by an hereditary unit; on the other hand, it seems even more probable that there is a continuous gradation in depth of pigmentation and that the strong internal conditions that lead to deeper pigmentation dominate over the weaker conditions. In the one case the varying characteristic is composed of a series of steps; in the other of an inclined plane. But a series of steps can not be distinguished from an inclined plane if the steps be taken small enough.

D. HEREDITY OF SKIN PIGMENTATION IN CROSSES BETWEEN WHITES AND NEGROES

The behavior in inheritance of the very dark skin pigmentation characteristic of negro races now deserves consideration. It is remarkable that despite the abundance of material available the facts of the inheritance of pigmentation in such crosses should have remained so long in dispute. To settle the question whether segregation occurs, two essential conditions must be met. First, the parentage of the children must be unquestioned and, second, the degree of pigmentation must be quantitatively expressed. Through the kind cooperation of correspondents in the south and above all of Professor H. E. Jordan, of the University of Virginia, who furnished all of the quantitative data, I am able to meet these conditions.

The quantitative data were obtained by means of the Bradley color top, using the standard colors of the Milton Bradley Company, of Springfield, Mass. The numbers given are percentages of the entire area of the disc occupied by the corresponding colors on the revolving disc. All color determinations were made of the dorsal aspect of the forearm slightly above the wrist. The determinations by the color top indicate that human skin color is obtained by mixing black (N), yellow (Y), red (R) and white (W). The first constituent is the melanic pigment, the second probably is due to a lipochrome pigment so wide-spread in animals and found in the human hair and iris, the red is chiefly that of hæmoglobin; and the white is reflected from the opaque skin. The color formula of the skin of the wrist of a slightly tanned "white" skin—the writer's—is as follows:

N	Y	R	W
8	9	50	33

The determinations by the color top are fairly delicate. The formula 10–12–41–37 gives a decidedly different color from the foregoing and not red enough for any wrist-skin. The skin color of a very dark negro, about 18 years old, measured by Dr. Jordan gave: N 75, Y 3, R 20, W 2. Dr. Jordan thinks the skin color of this boy's face would be given by N 90, R 10. Another black negro is given by N 68, Y 2, R 26, W 4.

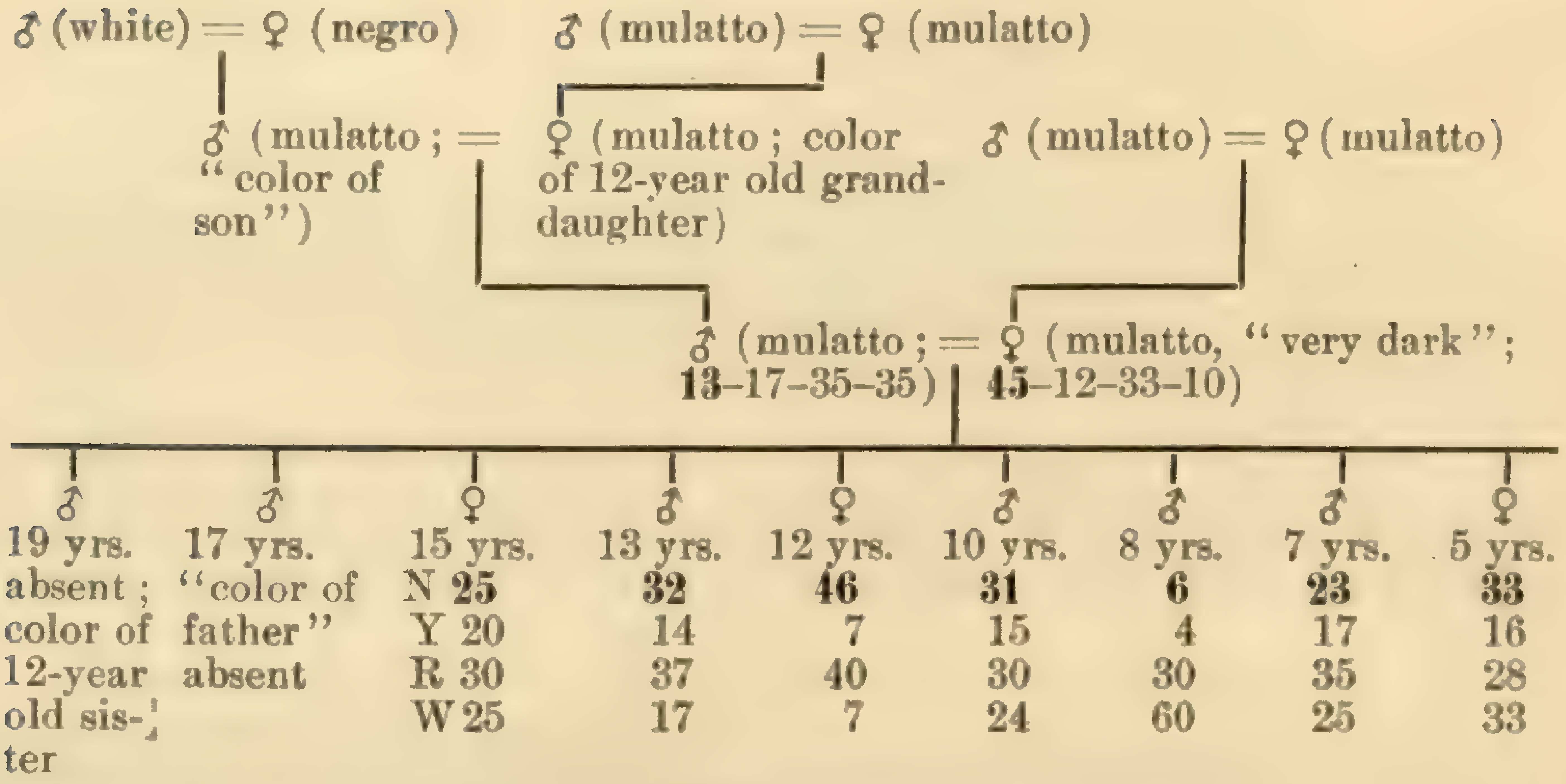
We may now consider the pedigrees of skin color collected by Dr. Jordan.

As to the question of legitimacy, Dr. Jordan writes: "There isn't the least doubt, I think, about the legitimacy of the children in the families of 'H.,' 'W.,' 'J.' and 'F.'[5]

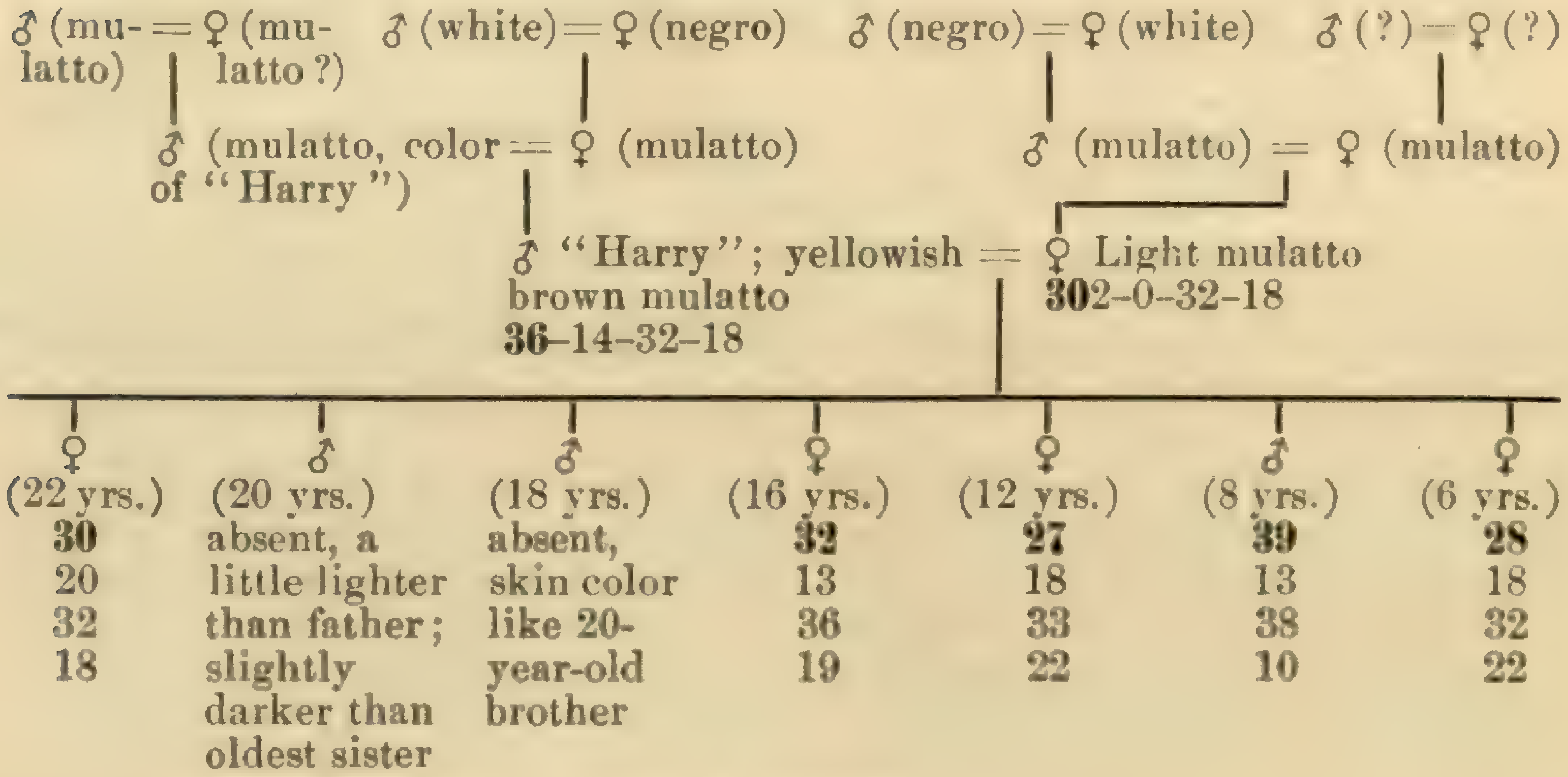
---

[5] The quantitative data on this family were not obtained, as the members were too inaccessible. The "C." family was obtained after Dr. Jordan's letter was written, and his remarks are doubtless applicable to that family also.

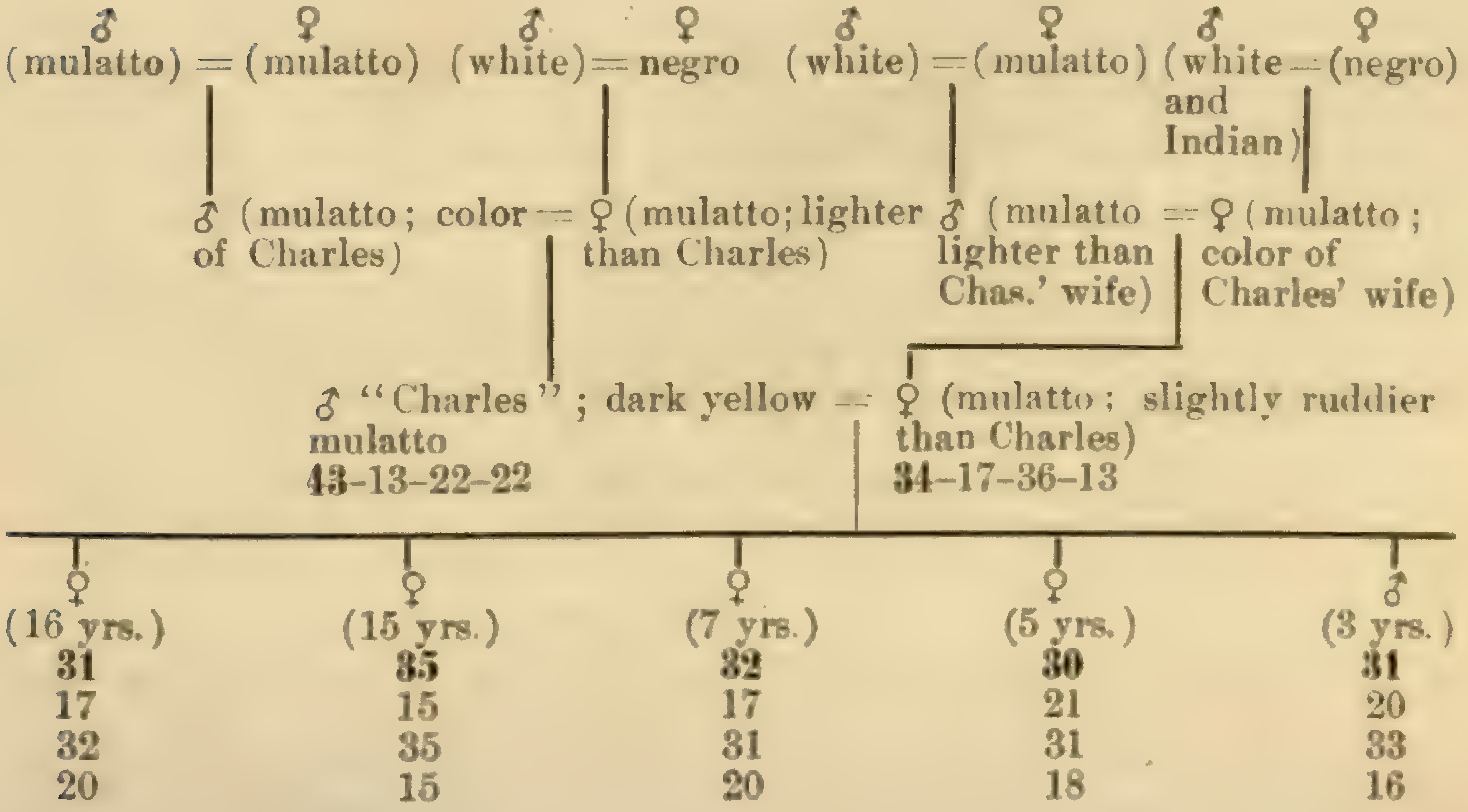
W. FAMILY


♂ (white) = ♀ (negro)
♂ (mulatto) = ♀ (mulatto)
♂ (mulatto; "color of son")
= ♀ (mulatto; color of 12-year old grand-daughter)
♂ (mulatto) = ♀ (mulatto)
♂ (mulatto; 13–17–35–35) = ♀ (mulatto, "very dark"; 45–12–33–10)
♂ 19 yrs. absent; color of 12-year old sister
♂ 17 yrs. "color of father" absent
♀ 15 yrs. N 25 Y 20 R 30 W 25
♂ 13 yrs. 32 14 37 17
♀ 12 yrs. 46 7 40 7
♂ 10 yrs. 31 15 30 24
♂ 8 yrs. 6 4 30 60
♂ 7 yrs. 23 17 35 25
♀ 5 yrs. 33 16 28 33

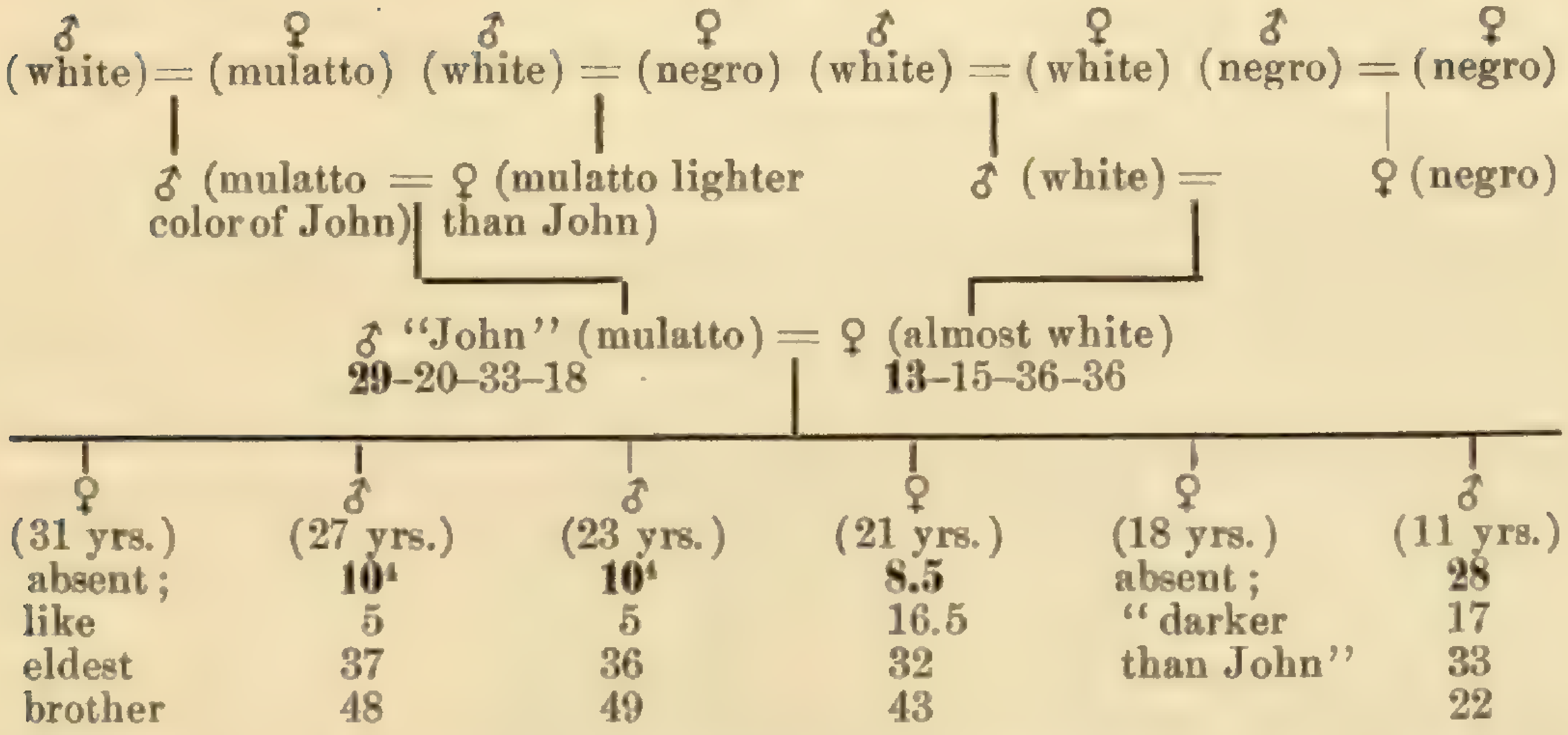
H. FAMILY


♂ (mulatto) = ♀ (mulatto ?)
♂ (white) = ♀ (negro)
♂ (negro) = ♀ (white)
♂ (?) = ♀ (?)
♂ (mulatto, color of "Harry") = ♀ (mulatto)
♂ (mulatto) = ♀ (mulatto)
♂ "Harry"; yellowish brown mulatto 36–14–32–18 = ♀ Light mulatto 302–0–32–18
♀ (22 yrs.) 30 20 32 18
♂ (20 yrs.) absent, a little lighter than father; slightly darker than oldest sister
♂ (18 yrs.) absent, skin color like 20-year-old brother
♀ (16 yrs.) 32 13 36 19
♀ (12 yrs.) 27 18 33 22
♂ (8 yrs.) 39 13 38 10
♀ (6 yrs.) 28 18 32 22

C. FAMILY


♂ (mulatto) = ♀ (mulatto)
♂ (white) = ♀ negro
♂ (white) = ♀ (mulatto)
♂ (white and Indian) = ♀ (negro)
♂ (mulatto; color of Charles) = ♀ (mulatto; lighter than Charles)
♂ (mulatto lighter than Chas.' wife) = ♀ (mulatto; color of Charles' wife)
♂ "Charles"; dark yellow mulatto 43–13–22–22 = ♀ (mulatto; slightly ruddier than Charles) 34–17–36–13
♀ (16 yrs.) 31 17 32 20
♀ (15 yrs.) 35 15 35 15
♀ (7 yrs.) 32 17 31 20
♀ (5 yrs.) 30 21 31 18
♂ (3 yrs.) 31 20 33 16

J. Family


♂ (white) = ♀ (mulatto)
♂ (white) = ♀ (negro)
♂ (white) = ♀ (white)
♂ (negro) = ♀ (negro)
♂ (mulatto color of John) = ♀ (mulatto lighter than John)
♂ (white) =
♀ (negro)
♂ "John" (mulatto) = ♀ (almost white)
29–20–33–18
13–15–36–36
♀ (31 yrs.) absent; like eldest brother
♂ (27 yrs.) 10[4] 5 37 48
♂ (23 yrs.) 10[4] 5 36 49
♀ (21 yrs.) 8.5 16.5 32 43
♀ (18 yrs.) absent; "darker than John"
♂ (11 yrs.) 28 17 33 22

Dr. F—— for years a resident of this section, and health officer of C——, supports me in this belief. Moreover, I have explained to each family the necessity for my study of absolute certainty on this point, have asked them the direct question, and each about the other, and can get only the assurance that the family life in each case is entirely chaste. One man is a minister, one principal of the colored school, one a thriving merchant and one a barber, and all seem considerably above the grade of morality and intelligence of the ordinary stupid and irresponsible negro. I think you may be absolutely certain regarding the chastity of the several mothers concerned." Those who know Dr. Jordan will appreciate the better the great weight to be given his conclusion. It seems to us we may proceed to discuss these cases as experimental data.

Of the four families the W. family is, perhaps, the most striking. The father, the grandson of a white man, has himself a grade of pigmentation (black, 13 per cent.) no darker than that of a brunet. His wife is very dark (black, 45 per cent.). The children range from white (black, 6 per cent.) to as dark as the mother (46 per cent.). The entire series of percentages of black runs: 6, 23, 25, 31, 32, 33, 46. We have here 1 light intermediate; 5 of mulatto tint and 1 "very dark." None of the children show a significantly greater pigmentation than the darker parent, and one is lighter than the lighter parent. There is clear evidence of segregation of the skin pigmentation.

---

[4] These measurements were made an hour apart, after shifting of the color discs and the later without recalling the earlier measurement.

The J. family is important because of the mating of an "almost white" first generation mulatto with a male mulatto who is more than twice as dark. Of the four children measured three are nearly white, whiter than the mother, and one is as dark as the father. The series runs: 8.5, 10, 10, 28. A segregation of practically white and half dark (grandparental colors) takes place here also.

The H. family has also several points of interest. A lighter and darker mulatto parent (black, 30 per cent. and 36 per cent., respectively) from four mulatto grandparents have children ranging in amount of black pigment from 27 to 39; these extremes being somewhat lighter and somewhat darker, respectively, than the parents. No white appears. This result is like that obtained in many Caucasian families with "intermediate" skin color; where two "intermediate" parents (that apparently do not have hypostatic "blond") breed true. They behave like "pure dominants."

The C. family gives much the same result. Two second generation mulattoes of rather dark type have children of this dark type only. None of them exceed the darker parent; some of them run lighter than the less pigmented parent. These parents also seem "pure dominants," or, better, contain no hypostatic white.

The significance of the data of these four families is perfectly clear in view of the studies that we have made on the inheritance of hair and skin color in "Caucasians." There are many grades of pigmentation—more or less definite stopping points, perhaps, in a continuous pigmentation process. A tendency to proceed far in the pigmentation process is dominant over the less progressive condition, but imperfectly so. Consequently, first-generation mulattoes are not as dark as the negro parent. Whether in the offspring of two such mulattoes the "extracted dominants" would ever return to the original pigmentation of the dark negro parent is doubtful; first, because neither "white" nor black is a single unit. Only in rare instances will the "extracted" blacks be free of some white unit. We are dealing in this case not with two unit characters only but perhaps with a myriad of them. A chance combination of a lot of lower grades will give "white" skin; a combination of "dark units" free of any "white units" would give a dark skin, but most of the offspring will show the various intermediate grades due to diverse combinations of the black and white units. As a rule, even in the first hybrid generation, the darkest grade that is potential in the protoplasm tends to show in the offspring; and so, as a general rule, offspring are rarely darker than the darker parent.

To the foregoing quantitative data may be added some qualitative evidence concerning inheritance of skin color in black × white crosses. This testimony is all that I have been able to collect of a definite nature and it has all come from persons possessed of negro blood.

Professor W. E. DuBois, of Atlanta University, Georgia, writes:

> Strictly speaking a mulatto is a child of a white person and a full-blooded negro. . . . [Their] children are liable to vary greatly. . . . They might be light in color or dark in color . . . or freckled, with red curly hair.

Maj. R. R. Moton, of the Hampton (Va.) Normal and Agricultural Institute, writes:

> Mulatto parents very often have children that are practically white so far as external appearances are concerned, and the same parents may have children that are black or very dark brown. This is very common. Indeed, I think it is more often that the children vary than not.

He cites three examples, all of families whose fathers hold positions of trust in Hampton; two in the institute. A. "is a mulatto and so is his wife. Their first child was a girl . . . a distinct blond in hair and complexion.

The second child was very dark, darker than either father or mother.'' B. ''is a mulatto and his first wife was a mulatto. Their first child, a girl, was . . . just the complexion of the father and mother. The second child, a boy, was very dark.'' C. ''is a mulatto, and his wife is also a mulatto. Their first child, a girl, is darker than either mother or father; not black, however. The second, a boy, is much lighter than either mother or father; almost white. The third, a girl, is a distinct blond with Saxon eyes and complexion.''

Professor T. B. Williams, of Hampton Institute, writes:

> I know two large families in which both parents in each family are practically white. All of the children are like the parents, practically white. In fact some of them have left home and are "passing for white" in other sections.

These cases are important as indicating that the lower grades of pigmentation do not produce the higher grades (except that some mulatto tints produce darker children by extraction of the white). Professor Williams continues:

> In another family the mother is practically white, the father, a mulatto, is darker. They have six girls. Five of them are practically white; one is a very light yellow. In another family the father and mother are as nearly pure mulattoes as are commonly found. One parent is in each case, I am pretty sure, white, and the other in each case is a pure or nearly pure negro. The children of this couple vary from the parents both ways. The older child is fairer than the parents and even has blue eyes, while theirs are dark. The younger child is darker than the parents, though not "black, or nearly so." I could multiply these illustrations may times. There are, too, settlements of mulatto people who for some generations have taken pains not to marry among darker colored people but have gone on intermarrying yet I have never seen a black person as a result of these unions.

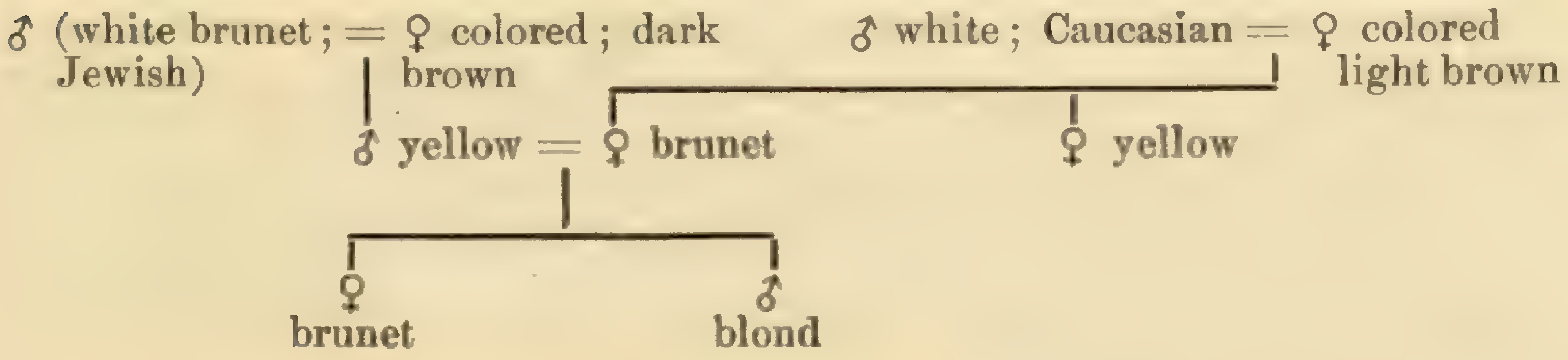
In addition to these data from colored people we have the following from Professor H. V. Wilson, of the University of North Carolina. The family was reported to him by a physician.

> Parents, fairly light mulattoes. Woman virtuous. Several children. All children but one, the ordinary type of mulatto; characteristics inter-

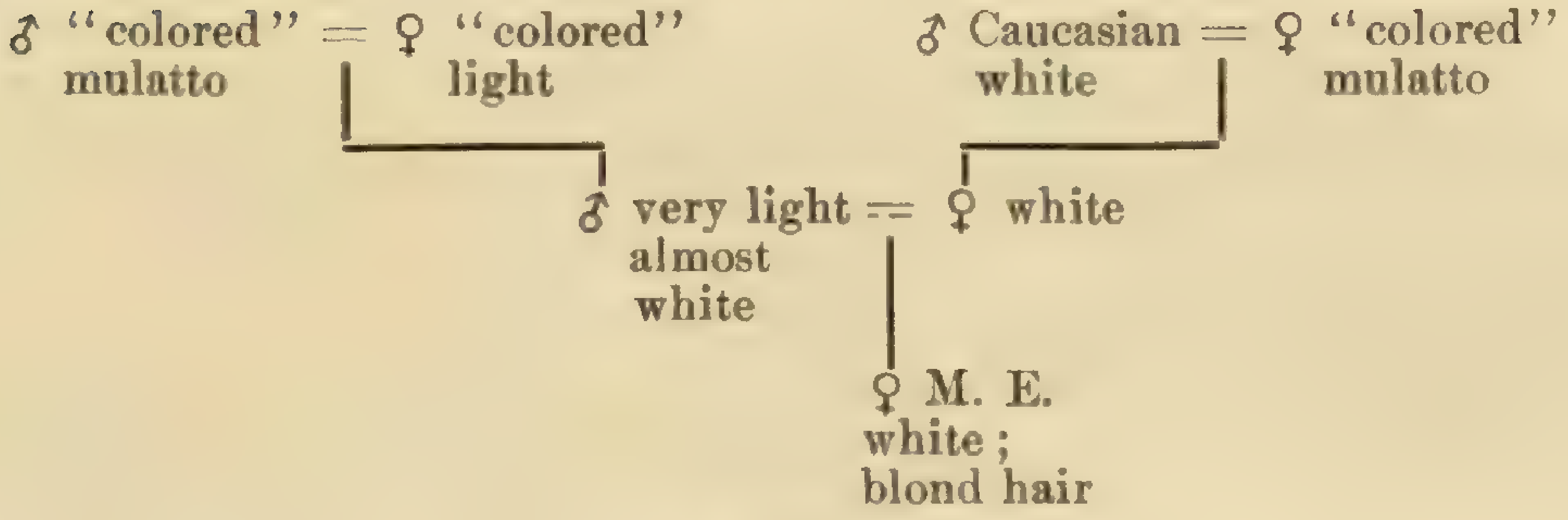
mediate between negro and white. One child shows segregated characters, has blue eyes and other characters close to those of white race.

Finally we give sundry fragments of pedigrees furnished by two reliable and highly intelligent colored persons. Owing to the slight social sentiment among most colored persons against unchastity, they have little motive to hide from one another the facts of parentage of children. Consequently the facts as given below are probably correct.

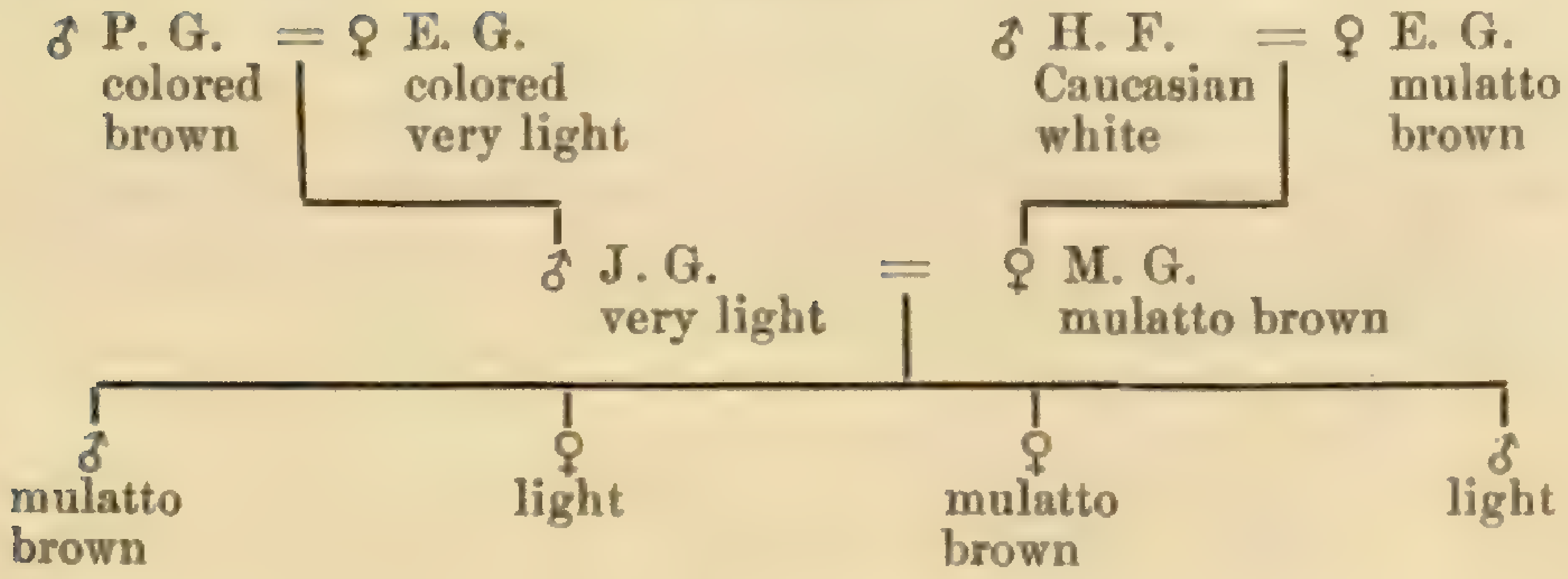
B. FAMILY


♂ (white brunet; Jewish)
♀ colored; dark brown
♂ white; Caucasian
♀ colored light brown
♂ yellow
♀ brunet
♀ yellow
♀ brunet
♂ blond

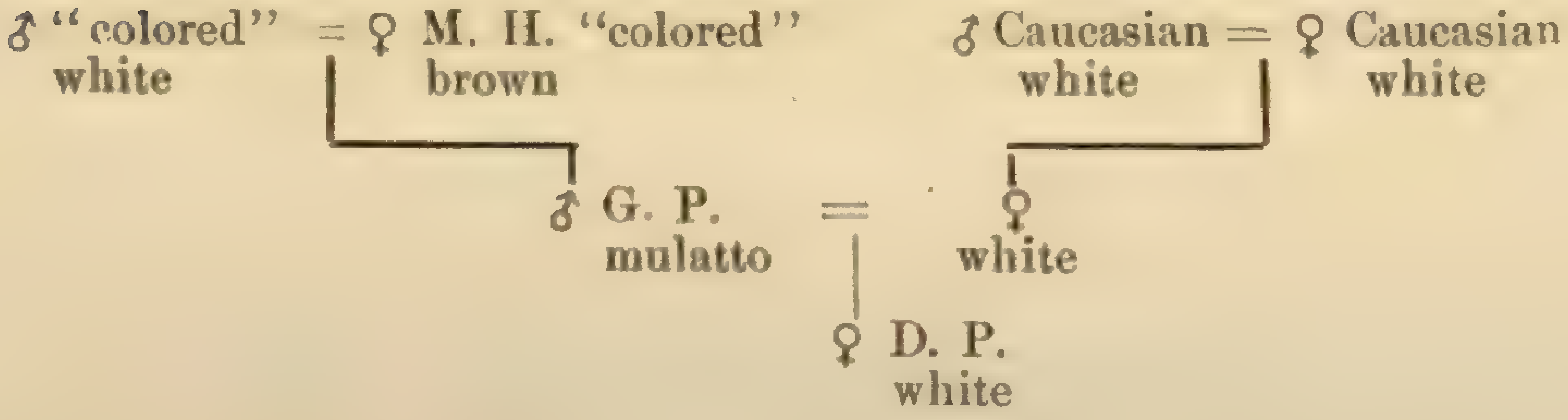
E. FAMILY


♂ "colored" mulatto
♀ "colored" light
♂ Caucasian white
♀ "colored" mulatto
♂ very light almost white
♀ white
♀ M. E. white; blond hair

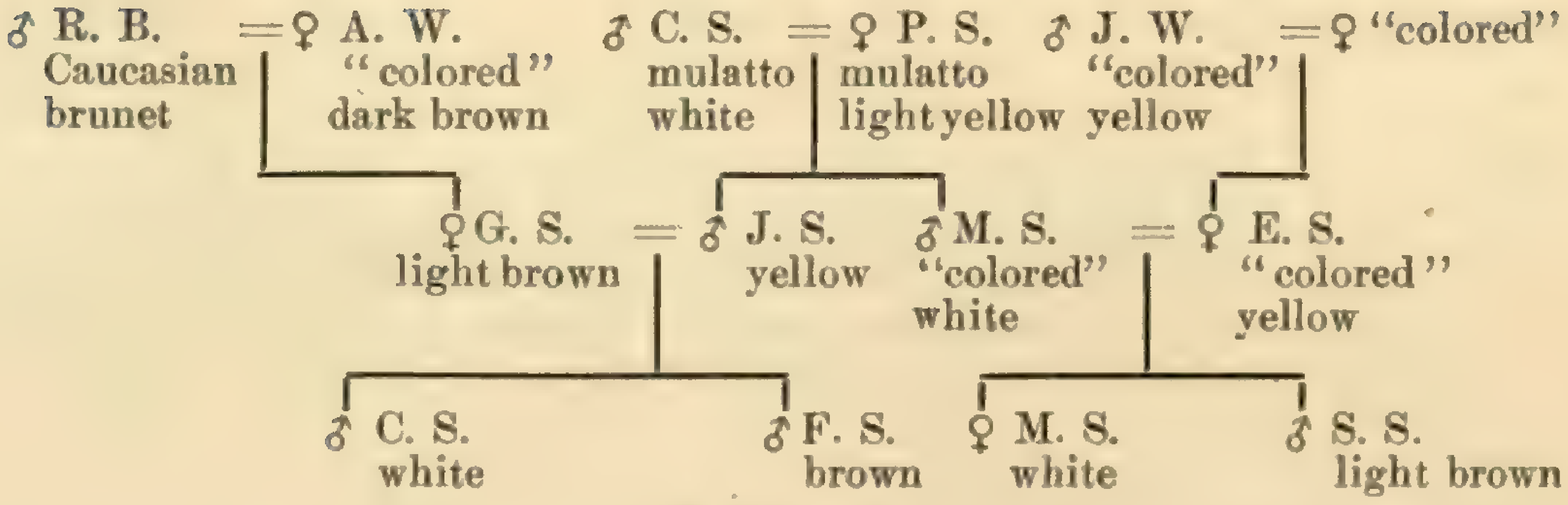
G. FAMILY


♂ P. G. colored brown
♀ E. G. colored very light
♂ H. F. Caucasian white
♀ E. G. mulatto brown
♂ J. G. very light
♀ M. G. mulatto brown
♂ mulatto brown
♀ light
♀ mulatto brown
♂ light

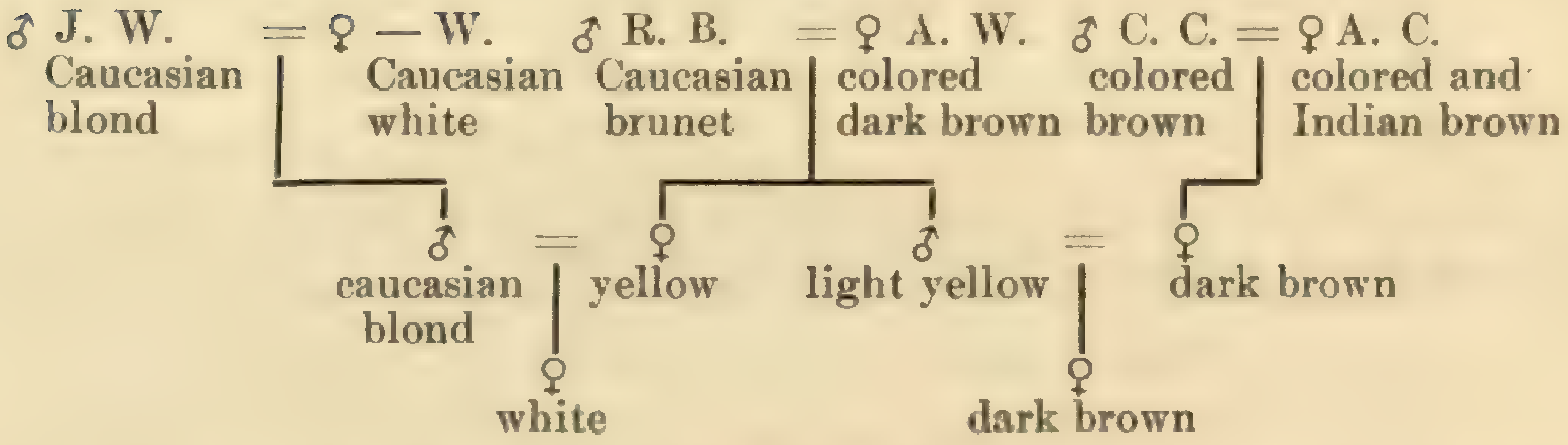
P. FAMILY


♂ "colored" white
♀ M. H. "colored" brown
♂ Caucasian white
♀ Caucasian white
♂ G. P. mulatto
♀ white
♀ D. P. white

S. Family

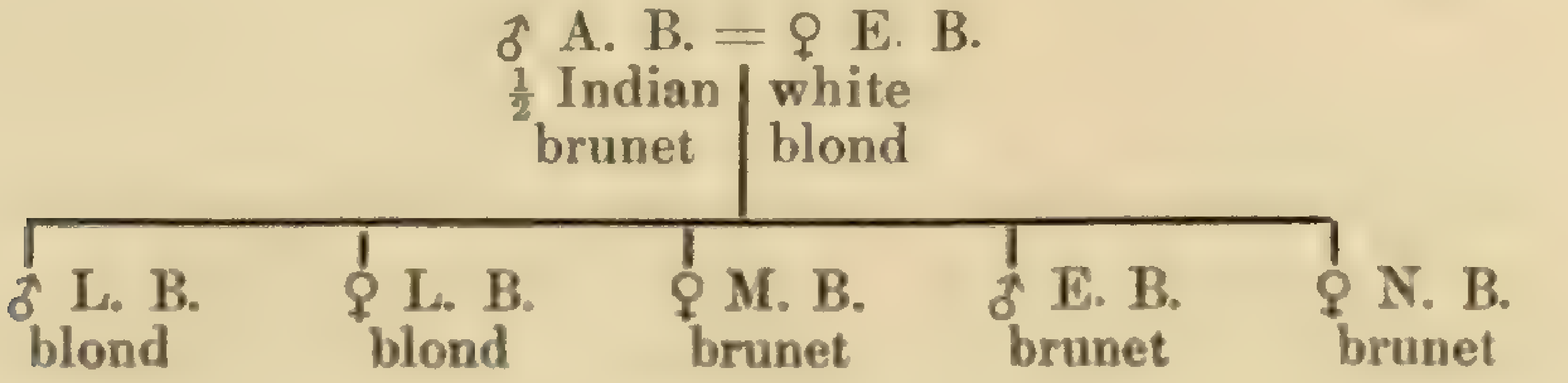

♂ R. B. Caucasian brunet
= ♀ A. W. "colored" dark brown
♂ C. S. mulatto white
= ♀ P. S. mulatto light yellow
♂ J. W. "colored" yellow
= ♀ "colored"
♀ G. S. light brown
= ♂ J. S. yellow
♂ M. S. "colored" white
= ♀ E. S. "colored" yellow
♂ C. S. white
♂ F. S. brown
♀ M. S. white
♂ S. S. light brown

W. Family

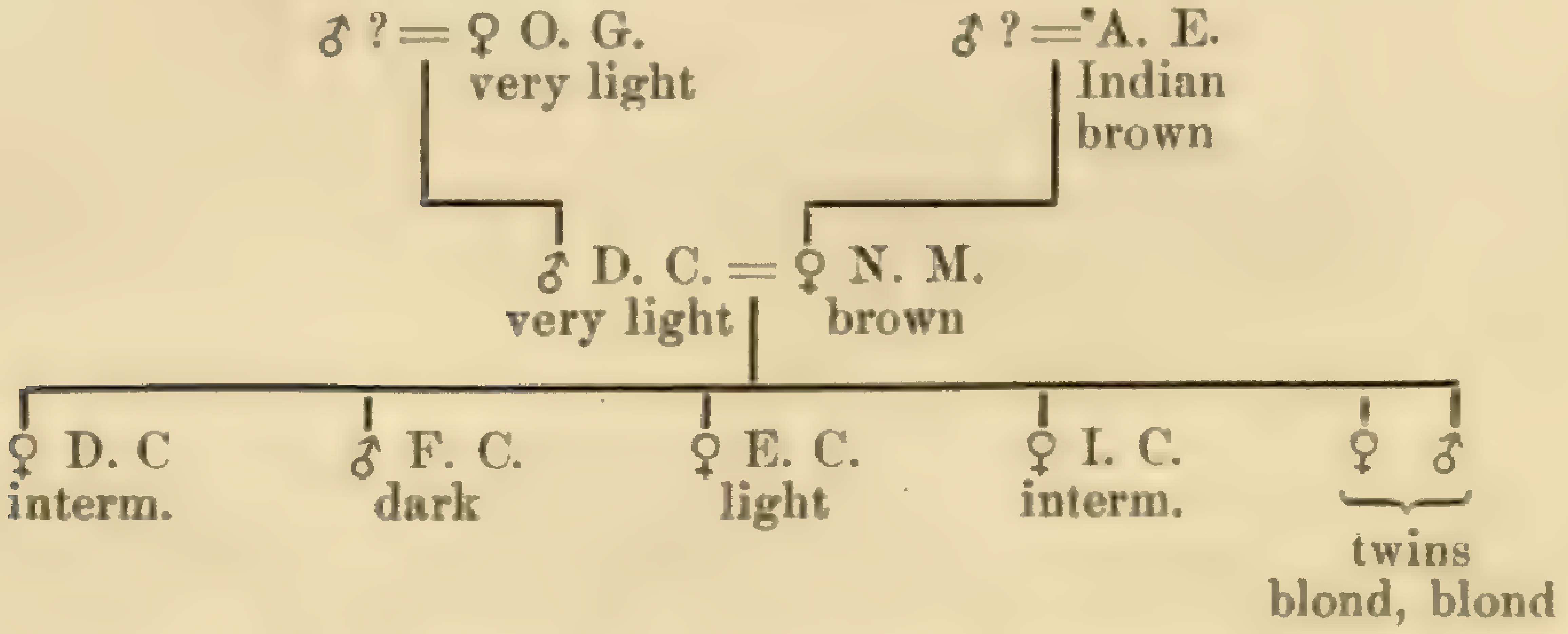

♂ J. W. Caucasian blond
= ♀ — W. Caucasian white
♂ R. B. Caucasian brunet
= ♀ A. W. colored dark brown
♂ C. C. colored brown
= ♀ A. C. colored and Indian brown
♂ caucasian blond
= ♀ yellow
♂ light yellow
= ♀ dark brown
♀ white
♀ dark brown

The following families are the product of North American Indian and white crosses.

Bes. Family


♂ A. B. ½ Indian brunet
= ♀ E. B. white blond
♂ L. B. blond
♀ L. B. blond
♀ M. B. brunet
♂ E. B. brunet
♀ N. B. brunet

Coo. Family


♂ ? = ♀ O. G. very light
♂ ? = A. E. Indian brown
♂ D. C. very light
= ♀ N. M. brown
♀ D. C interm.
♂ F. C. dark
♀ E. C. light
♀ I. C. interm.
♀ ♂
twins blond, blond

In some of these families segregation is apparent, notably, in B., G. and S., and Bes and Coo.

Finally, we may refer to an observation made by Louis Agassiz (1891, p. 532) in Brazil which bears upon the matter of segregation, both of skin color and other characteristics. After referring to the striking differences between the white × negro, the Indian × negro and the Indian × white hybrids, and stating that the Indian characters are the more deeply impressed on the offspring, he says:

> I have known the offspring of an hybrid between Indian and negro with an hybrid between Indian and white resume almost completely the characteristics of the pure Indian.

The conclusion from these various data, qualitative as well as quantitative, is that skin color in negro × white crosses is not a typical "blend" as conceived by those who oppose the modern direction of research in heredity, but that, on the contrary, the original grades of heavy and slight melanogenesis segregate in the germ cells—often imperfectly because of the multiplicity of units (or grades) for skin pigmentation—and thus the original color characters are more or less perfectly restored. All studies indicate that blonds lack one or more units that brunets possess; that the negro skin possesses still additional units; that individuals with the heavier skin pigmentation may have slight pigmentation covered over—hypostatic, evidence of this condition appearing in the light offspring of such hybrids in the second or third generation; and that first-generation hybrids frequently show, somatically, a color grade less than that which they carry potentially and may segregate in their germ cells.

(To be concluded)

THE COLOR SENSE OF THE HONEY-BEE: CAN BEES DISTINGUISH COLORS?

JOHN H. LOVELL

CAN bees distinguish between differently colored floral leaves? If they can not, then, a polychromatic flora possesses no advantage over one in which the flowers are all of the same hue. In the Alpine flora, says Kerner, on the heights above the tree-line, there is actually no spring and no autumn, only a short summer following a long winter. All the flowers have, therefore, to blossom in a short time. "White and red, yellow and blue, brown and green, stand in varied combination on a hand's-breadth of space."[1] These color contrasts, it is believed, enable bees easily to remain constant to a single plant species so that pollination is effected to the mutual advantage of both insects and flowers. If the flowers were visited indiscriminately, regardless of their form, much pollen would be wasted and not a little time and effort would be lost. Genera adapted to bees, according to Müller, display a variety of colors, especially when they bloom simultaneously in the same locality, as *Aconitum lycoctonum* yellow, *A. napellus* blue; *Lamium album* white, *L. maculatum* red, *Galeobdolon luteum* yellow; *Salvia glutinosa* yellow, *S. pratensis* blue; *Pedicularis tuberosa* whitish yellow, *P. verticillata* purple.

> If the different colors were evolved, as I believe, because of the power and necessity in bees of discriminating between them then it is not wonderful to find represented among bee flowers not only white, yellow, red, violet, blue, brown and even blackish (*Bartsia*) in the most varied degrees, but also to see several colors in the same flower combined in manifold ways. I mention only *Polygala Chamæbuxus, Viola tricolor,*

---

[1] Kerner, Anton, "Natural History of Plants," translated by F. W. Oliver, 2, pt. 1, 198. Also see Plate XII., "Alpine Flowers in the Tyrol," drawn from nature by E. Heyn.

Cerinthe major, Galeopsis versicolor, Astragalus depressus, alpinus and many other Papilionaceæ.[2]

On the other hand, it is asserted by Plateau that all natural flowers might be as green as their leaves without their pollination by insects being compromised;[3] while in the opinion of Bethe bees are mere reflex machines and have no senses, or ability to make experiences and modify by them their actions.[4] If either of these extreme claims is admitted, it is evident that a variety of colors can be of no benefit to flowers. It seems desirable, therefore, to consider what experimental evidence is available to prove that bees can distinguish differences in color.

It was first shown by Lubbock (Lord Avebury) that honey-bees can distinguish between "artificial" colors, or slips of paper of different hues. An account of his experiments is given at considerable length in his well-known book on "Ants, Bees and Wasps"; but, as they were performed more than thirty years ago, I shall describe a number of experiments made myself, in some of which the conditions have been varied. I shall endeavor to show not only that bees can distinguish between the colors of papers, of flowers and of painted hives, but that they can learn *not to discriminate* between them, when this is for their advantage. Their behavior in detail will likewise be carefully recorded.

On a pleasant September morning I accustomed a yellow (Italian) bee to visit a strip of blue paper[5] three inches long by one inch wide. To prevent the paper from blowing away or becoming soiled it was covered with a transparent glass slide of the same dimensions, upon the center of which a small quantity of honey was placed. These slides are used for mounting microscopic objects, and may be obtained of any dealer in optical instruments for a trifling sum.

---

[2] Müller, Hermann, "Alpenblumen," p. 500. Knuth, Paul, "Handbuch der Blütenbiologie," 1, 141, or "Handbook of Flower Pollination," translated by J. R. Ainsworth Davis, 1, 117.

[3] Plateau, Félix, "Les insectes et la couleur des fleurs," *L'Année Psychologique*, 13, 79.

[4] Buttel-Reepen, H. v., "Are Bees Reflex Machines?" translated by Mary H. Geisler, p. 3. Bethe, Albrecht, "Dürfen wir den Ameisen und Bienen psychische Qualitäten zuschreiben?" p. 86. Emil Strauss, Bonn, 1898.

[5] The colored papers used were obtained from the Milton Bradley Co., Springfield, Mass., and were produced in pure spectrum colors by having the surface coated. Stained papers have the colors somewhat broken.

After the bee had made a number of visits to the blue paper, a red slide of the same dimensions, and prepared as described above, was placed six inches to the right of it. An equal quantity of honey was also placed upon the center of this slide. When the bee returned from the hive it alighted on the blue slide, which still remained in its original position.

On the departure of the bee for the hive the slides were transposed, *i. e.*, the red put in the place of the blue and the blue where the red had been. When the bee returned, and no longer found the blue paper in its usual position, it flew back and forth, examining both slides, paused for a second or two on the red, then resumed its flight, but finally settled on the blue. A little later it flew up into the air, but soon returned to the blue; then it flew across to the red, where it remained for the rest of its visit. The change in the position of the blue, and the discovery of a differently colored slide also bearing honey, evidently disturbed the bee; and its frequent flights showed that it was endeavoring to orient itself to these new conditions. As will now appear it did not find it necessary to repeat this course of reconnoitering.

While the bee was away I transposed the slides for a second time, the distance apart being as before—six inches. The bee returned directly to the blue. Twice it left the blue for a few moments, but each time returned to it.

When the bee left for the hive, I again transposed the slides; the bee returned to the blue. The bee left for the hive, and I transposed the slides. It returned to the blue.

While the bee was away I transposed the slides for the fifth time. The bee returned to the blue. Then it left the blue slide, flew across to the red, but at once returned to the blue.

The bee left for the hive and I transposed the slides. On its return it circled about as though in doubt and presently disappeared from view; but a little later it returned and settled on the blue. While taking up its load of honey it left the blue three times, but in each instance returned.

The bee left for the hive and I transposed the slides. It returned to the blue.

The bee left for the hive and I transposed the slides for the eighth time. On returning the bee hovered close to the red, and then went to the blue.

As soon as the bee returned to the hive, I transposed the slides for the ninth and last time. When the bee came back, it alighted after a little hesitation on the blue. It left once and flew across to the red, but soon returned to the blue. Left a second time but soon returned. Then it flew into the room, and on being released went back to the hive.

There can be no question that in this experiment the honey-bee was able to distinguish the blue color from the red. I repeated the experiment many times and varied it in many different ways, but the bee always showed its ability to distinguish between differently colored slips of paper. Only one bee should be employed, for if there are two or three they will conflict and to some extent produce confusion.

For the purpose of comparison the following experiment, in which a larger number of colored slides was employed, was performed on the morning of September 20, six days after the experiment just related. A black or German bee, instead of an Italian bee as before, was accustomed to visit a blue slide prepared as described above. After a number of visits had been made, the blue slide was moved to the right about seven inches, and a red slide put in its place. The bee returned to the blue.

As soon as the bee left for the hive, the slides were transposed. The bee returned to the blue. The bee again left for the hive and I transposed the slides. It returned to the blue.

When the bee left for the hive, I transposed the slides for the fourth time. The bee returned to the red, which was now in the place occupied by the blue at the time of its previous visit.

The bee left for the hive, but no change was made in the position of the slides. On its return it again sought the blue, showing that the influence of this color was still dominant, though it now knew from memory as well as from its visual and olfactory senses that honey was to be found on the red.

A yellow slide was now placed upon the board about seven inches to the left of the blue. The order of the colors was yellow, blue, red, and their distance apart seven inches. The bee returned to the blue. When the bee left, I transposed the yellow and blue so that the order was blue, yellow, red. The bee returned to the blue. On the departure of the bee I again transposed blue and yellow. The bee returned to the blue.

When the bee left for the hive, a white slide was introduced and the distances between the slides reduced to four and one-half inches. The order of colors was yellow, white, blue, red. The bee on its return flew back and forth several times over the slides, and after hovering in the air for a few moments in hesitation alighted on the white.

The bee left for the hive, but no change was made in the order of the slides; it returned to the blue.

When the bee left, a black slide was substituted for the white one. The order of the slides was yellow, black, blue, red and the distances apart remained as before four and one-half inches. The bee returned to the yellow, but soon left it (perhaps disturbed by a fly) and returned to the blue. No change was made in the order of the slides, and the bee returned to the black. But on its next visit it again sought the blue.

I now transposed the red and blue, bringing blue to the extreme right so that the order was yellow, black, red, blue. The bee returned to the blue. The red and blue were again transposed, the bee returned to the black, but soon left it for the blue. Black and blue were then transposed, the bee returned to the blue. I next transposed yellow and blue, bringing blue to the extreme left, the bee returned to the red. No change was made in the order of the slides, the bee returned to the yellow. The slides were again left unchanged, the bee touched on black, then on red, but finally alighted on blue. Red and blue were transposed so that the order of colors was red, yellow, black, blue. The bee returned to the black. No change was made in the slides, the bee returned to the blue.

During the first five visits, when there were only blue and red slides, the bee returned four time to the blue and but once to the red. This single exception is not without value, since it shows that the bee had the power of choice, and that its behavior was not mechanical, or that of a reflex machine. During the next three visits blue, red and yellow slides were employed and the bee returned every time to the blue. During the following thirteen visits four slides were used (blue, red, yellow, white in two visits; blue, red, yellow, black in eleven visits), and the bee naturally showed greater hesitation and an increasing tendency to visit other colors than blue. Still it took up its load eight times on blue to once on white, once on red, once on yellow, and twice on black. In every instance where the bee selected another color than blue, it will be observed that it was after the slides had been transposed, or a color had been changed; and that with one exception it again returned to blue on the next visit. Of the total twenty-one visits fifteen were made to the blue, but not more than two to any other color. The bee steadily endeavored to remain constant to the blue, though this involved both loss of time and effort; and the number of exceptions is surprisingly few when we remember that before the close of the experiment the bee had learned from experience that there was an ample supply of amber-colored honey on each of the four slides.

The purpose of my next experiment was to determine whether bees could readily determine a colored slide from a plain glass one. On September 10, 1908, I accustomed a line of Italian bees to visit a yellow slide. I then moved it six inches to one side, and exactly in its place I put a glass slide, under which there was no colored paper. A small quantity of honey was placed on the center of each slide. During twenty minutes the bees were carefully watched, and twelve visits to the yellow slide were recorded. A species of *Vespa* had built a nest not far away, and some of the workers also came to the yellow slide, and although they were an extraneous or foreign factor not directly connected with the experiment, their behavior was not without interest. Near the end of the time mentioned one of the wasps discovered the honey on the colorless slide and subsequently visited it. A bee attracted apparently by the presence of the wasp on this slide alighted beside it, but after a few moments flew across to the yellow.

I now transposed the slides, the distance apart remaining six inches as before. During ten minutes the Italian bees made eight and the wasps nine visits to the yellow slide. Only one visit was made to the colorless slide and that was by a wasp. Another wasp alighted on the colorless slide for a few moments before going to the yellow. There were a number of visits made by flies, all of which were to the yellow. In this experiment not only was the colored slide easily distinguished from the one without color, but it was apparently more attractive not alone to the bees, which had been trained to visit it, but to incidental visitors such as the wasps and flies. There were, moreover, no exceptions to the fidelity of the bees to the yellow color, as there were in the earlier experiments, when they were given the choice between two colors.

The preference of the bees for the yellow slide was, indeed, so marked that possibly it might be objected that the plain glass slide was invisible, or at least very inconspicuous. Such a supposition would be a mistake, for while it was certainly less conspicuous than the yellow slip, it could yet be seen clearly by the aid of reflected light and the amber-colored honey at a distance of more than ten feet. A year later on October 11, 1909, this was established by experiment. Two black bees were trained to visit a plain glass slide. While they were absent, the slide was moved six inches to the right, and a blue slide, which owed its color to the floral leaves of the bee-larkspur (*Delphinium elatum*) was put in its place. One of the bees returned to the colorless slide. When it left I moved the colorless slide twelve inches to the right of the blue slide. In this position the bees visited it twice. I transposed the slides. Both bees returned to the colorless slide, and a little later one of them came again. As no visits had been made to the blue slide, there could be no question but that the bees saw the plain glass slide.

As the result of his experiments with artificial flowers Plateau assumes that the artificial colors of paper or of cloth appear to bees of a different tint or tone than do the colors of natural flowers, which to human eyes are apparently of the same hue.[6] My own investigations lead me to believe that this assumption is not well founded, and is not required to explain the behavior of bees under the conditions described by Plateau. The discussion of this question, however, would lead to too long a digression from the subject under consideration, and must be deferred to some other opportunity. But in passing it may be remarked that the readiness with which Bethe and his followers assume new forces and powers to sustain theoretical positions is not a little amazing to the prosaic naturalist content to work with known factors.[7]

---

[6] Plateau, F., "Les insectes et la couleur des fleurs," *L'Année Psychologique*, 13, 77. "Comment les fleurs attirent les insectes," 5th part, *Bull. Acad. roy. Bel.*, 3^{me} série, 34, 847–881, 1897. "Les fleurs artificielles et les insectes," *Mem. Acad. roy. Bel.*, 2^{me} série, 1, 3–103.

[7] Bethe holds that the bees are led back to the hive by a wholly unknown force. "Dürfen wir Ameisen und Bienen psychische Qualitäten zuschreiben?" p. 77, Bonn, 1898.

There is the less need of delay for inquiring into this imaginary power of vision, since bees as easily distinguish between the colors of flowers as between those of colored papers.

As the result of more than twenty-six hundred experiments on the color sense of the honey-bee Hermann Müller was convinced not alone that they could distinguish colors, but that they exhibited color preference.[8] Instead of colored paper he made use of floral leaves, which he placed between two object slides, the edges of which were afterwards sealed with a soluble gum. The slides employed by myself were made as follows: A grayish-white slip of cardboard three inches long by one wide was covered with the yellow rays of a garden sunflower, over which a glass slide of the same dimensions was placed and tied firmly with black silk thread. In like manner a blue slide was prepared from the blue perianth of the bee-larkspur (*Delphinium elatum*), and a red slide from three bright red flowers of the Zanzibar balsam (*Impatiens sultani*).

On September 29 I accustomed several yellow or Italian bees to visit the yellow or sunflower slide. The slide was then moved eight inches to the right, and in its place was put the blue slide made from the floral leaves of the bee-larkspur. There was a small quantity of honey as usual on the center of each slide. At the same time I removed three of the bees, leaving only one. The time was 3 o'clock P.M., and the slides were in the shade. The bee returned to the yellow.

The bee left for the hive, and I transposed the slides. It returned to the yellow.

The bee left for the hive, and I transposed the slides. It returned to the blue.

When the bee left for the hive, no change was made. It returned to the yellow.

As soon as the bee left for the hive I transposed the slides for the fifth time. Two bees returned, one of which alighted on the yellow, the other on the blue. There could be little doubt that the bee which alighted on the yellow was the one which was under observation. This decision was based partly on its appearance (young bees can easily be distinguished from old ones), and partly because it was probable that it would return to the yellow. Its subsequent behavior satisfied me that this conclusion was correct. The bee on the blue was removed.

---

[8] Müller, H., "Versuche über die Farbenliebhaberei der Honigbiene," *Kosmos*, 11, 273–99. Reprinted as a separate by R. Friedländer & Sohn, Berlin, 1883.

The bee on the yellow left for the hive and I transposed the slides. It returned to the yellow.

The bee left for the hive and I transposed the slides. The bee returned to the yellow, but presently left it, described a few circles in the air, and then again settled on the yellow.

The bee left for the hive, and I transposed the slides for the eighth time. The bee returned to the blue, but soon left it, and after circling around in the air alighted on the yellow, where it remained.

The bee left for the hive and I transposed the slides. It returned to the yellow.

During ten visits in only one instance did it take up its load on the blue. The dominant power of the yellow color is well shown in the case where the bee alighted on the blue, on which there was an abundance of honey, but soon left it for the yellow. In many other experiments, in which the red slide was used as well as the yellow and blue, the bees as easily discriminated between natural colors as between those which were artificial.

On October 6 I performed the following experiment for the purpose of determining whether bees were more strongly influenced by a colored slide than by one without color. A red slide, prepared from the bright red flowers of *Impatiens sultani,* an exotic from Zanzibar, was placed on a white box in the sun and about a dozen bees were permitted to visit it for some time. Each of the blossoms was an inch in diameter. At 10 o'clock in the morning a plain glass slide was substituted for the red one, which was moved six inches to the right. There was a liberal supply of honey on the center of both slides.

In a few minutes there were seven bees on the red slide and two on the colorless. The bees were now driven away, the slides transposed, and the distance apart increased to sixteen inches. Six bees and a fly (*Eristalis tenax*) soon came to the red slide, but only one bee came to the colorless. The number of bees on the red slide continued to increase until there were about eight,[9] and it was difficult for some of them to reach the honey. In the meantime there were only two bees on the colorless slide.

The bees were again driven away and the slides transposed, the distance apart remaining sixteen inches. At the end of a few moments there were eight bees on the red glass, and one bee on the colorless. The slides were transposed, and once more eight bees and the syrphid fly came to the red, and only one bee to the colorless.

The bees were driven away, and the slides transposed. Very quickly five bees selected the red, and two bees and the syrphid fly the colorless. Later there were eleven bees on the red, and only two on the colorless. The bees on the red slide were so crowded that this may have had some influence in sending two of them to the colorless. The honey on the latter slide was amber-colored and could be seen at a distance of twelve feet, while at times its odor must have been stronger than that upon the red slide, since it was removed much more slowly.

It may be objected that the very marked preference shown by the bees for the red slide was the result of their having been accustomed to visit it first. If one bee had been employed, this might be admitted, but in the case of so many bees, it is improbable, since they would naturally avoid continually crowding and interfering with each other. If, however, the objection is well founded, then they should continue to give the preference to the red slide, when a bright-colored slide is substituted for the colorless one.

---

[9] As the bees were closely bunched together, and were frequently coming and going, it was impossible at this moment to count the exact number within one.

Accordingly a blue slide was substituted for the one without color, and at the same time the slides were transposed, the distance apart still remaining sixteen inches. The honey was disposed as a narrow band along the center of each slide in order that it might be more easily accessible to the bees. In ten minutes there were eight bees on the red and two on the blue. A little later there were ten bees on the red, and four bees and a wasp on the blue.

The bees were driven away and the slides transposed. In a few minutes there were three bees and a wasp on the red, and nine bees on the blue. Ten minutes later there were six bees and an *Eristalis tenax* on the red, and four bees on the blue. Two minutes later there were three bees and the syrphid fly on the red, and seven bees on the blue. Very quickly then after the blue slide was substituted for the colorless one, the bees ceased to exhibit a preference for the red slide, and sometimes visited the red and sometimes the blue in larger numbers. This experiment thus affords evidence not only that bees can distinguish colors, but that they are also influenced by conspicuousness.[10]

The experience of apiarists furnishes very conclusive evidence of the power of bees to distinguish colors. The hives are sometimes painted different colors in order that the bees may mark their location with greater certainty and avoid entering the wrong hive. A bee-keeper describes in *Gleanings in Bee Culture* how he painted his hives red, white and blue, in order that the bees might mark their location largely by color. I have, he states, adopted the red, white and blue plan, since 1880, and am so well pleased with the result that I am painting all my new hives this spring in the same colors. It enables the bees to avoid making mistakes and going into the wrong hives. If you remove a white hive, many of the bees will pass the blue one on the one side and the red one on the other side, and go into the white hives further on. This shows conclusively that bees mark the position of the hive by color as well as by its environment.

---

[10] Lovell, John H., "The Color Sense of the Honey-bee: Is Conspicuousness an Advantage to Flowers?" AM. NAT., 43, 338–349, June, 1909.

> I admit that where a few colonies are kept in one place there is very little danger of the bees mixing; but where you have long rows of hives in sheds, as we have in Salt River Valley, the three colors will avoid a great deal of confusion and save the lives of many bees and some young queens.[11]

While this plan works admirably so long as the hives are not moved, it of course, gives very unsatisfactory results, if for any reason a hive is removed and one of another color is substituted for it. When a colony swarms naturally, says another apiarist, or is swarmed artificially, or for any reason the old hive body is removed, unless the new hive is of the same color as the old hive many of the bees will not return to it, but will scatter among the hives nearest to the old location, which are of the same color as the hive which has been removed. For example if the dwelling of the parent colony was white and if at the time of swarming an attempt was made to put the swarm in a blue hive a large part of the bees would refuse to enter it and would fly away to the nearest white hive, with the result that the new colony was materially weakened. He, therefore, found it more convenient to paint all his hives one color.[12]

Another bee-keeper placed his hives in two house-apiaries, each containing 150 colonies. The three end hives at each end of the shed or house were painted green. If now all the green hives at one end were removed, the bees instead of entering the hives nearest to the old location, which were painted a different color, flew to the green hives at the other end of the house apiary, and tried to enter them, even though they were closed.[13]

---

[11] Lessing, Wm., ''Painting Hives,'' *Gleanings in Bee Culture*, 34, 1428, November 15, 1906. For this article I am indebted to Mr. H. H. Root, editor of *Gleanings in Bee Culture*.

[12] Kinyon, Irving, ''Color of Hives; A Variety of Colors Undesirable,'' *Gleanings in Bee Culture*, 35, 262, February 15, 1907. Mr. Kinyon writes me that about one third to one half of a swarm would thus be lost.

These statements are confirmed by the experience of W. Z. Hutchinson, an authoritative writer on American apiculture.

> One spring I bought and brought home about forty colonies or hives painted a very dark gray, or almost lead color. They were set down in the apiary by themselves in four different rows. In the course of a few days I began transferring the bees from these hives into white hives, like the rest of the hives in my apiary. I took an end hive first. When the brood combs were set over into a white hive, and this hive set down where the old gray hive had been, the bees refused to enter it, but piled into the next hive in the row, which, of course, was gray like their old home. This hive was soon filled to overflowing, some of the bees hanging on the outside. I then transferred the combs from this hive to a white one, but the bees refused to enter it and piled into the next gray hive in the row. The hives were about three feet apart in the row. A bee is guided to its home by location as well as color, and after about four hives, or colonies, had been transferred, then some of the bees began to enter the new, white hives, as the gray hives were now so far from their old location that they perceived that they could not be their home. The same trouble was had in each row that was transferred.[14]

An excellent illustration of the effect of differently colored hives is given by Buttel-Reepen:

> A weak afterswarm, mostly of young bees from a hive painted blue, dispersed among the masses of humming bees which were just taking their flight of orientation out of the other hives (which, as is usually the case in Germany, Switzerland and Austria, were standing close together), and settled here and there in little clumps. After a short time they flew back to the bee-house; but only a few found the right hive; the rest flew to other colonies, and to which? Only where a blue door invited them did they attempt an entrance but nowhere else. Unfortunately they were so hostilely received that the ground in front of all the hives marked blue was covered with dead bees.[15]

The experience of apiarists, therefore, both in America and Europe furnishes indubitable evidence that bees by thousands readily distinguish colors.

---

[13] The experience of a neighbor of Mr. Kinyon and described by him in a letter to the writer.

[14] W. Z. Hutchinson, editor of *Bee Keeper's Review* and author of "Advanced Bee Culture" in a letter to the writer.

[15] Buttel-Reepen, "Are Bees Reflex Machines?" p. 38, translated by Mary H. Geisler.

Additional observations might easily be given, but those presented appear sufficiently conclusive. It has been shown that bees can distinguish between the colors of papers, of flowers, and of painted hives, and that they are more strongly influenced by a colored slide than by a plain glass one. It may well be doubted whether they would ever have been capable of making long journeys afield for nectar and pollen, if this visual power had been wanting. To those unfamiliar with the habits of bees, it will occasion surprise that the bee after it had discovered and began sucking honey on the red slide (to take for illustration the ninth visit of the first experiment) should have voluntarily left it and gone back to the blue for the larger part of its load. But its behavior in this instance is quite in accord with the principles of bee psychology. Bees, as Forel states as the result of his own and the experience of Huber, Buttel-Reepen and Wasmann, very rapidly form habits, and their attention becoming fixed by frequent repetitions is not easily diverted.[16] When the bee, which had been trained to visit the blue slide, alighted on the red, it was disturbed by the difference of hue and suffered a certain degree of mental disquietude, which was not allayed until it returned to the blue.

All of the higher Hymenoptera probably possess the power of distinguishing colors. This has been established for the social wasps of the genus *Vespa* by the interesting experiments of the Peckhams. One of their experiments very strikingly shows the value of color contrasts, and effectively refutes Plateau's assertion that all flowers might be as green as their leaves without their pollination being compromised.

> We once placed some dark red nasturtiums on light yellow paper near the nest, and found that more than one third of the homecoming wasps flew to them and hovered over them before entering. When light yellow nasturtiums, nearly matching the paper in color, were substituted only one out of thirty-six noticed them; and as the odor was as strong in

---

[16] Forel, August, "Ants and Some Other Insects," translated by William Morton Wheeler, p. 20.

one case as the other, it would seem that the color was the attracting force.[17]

It remains to consider the numerous instances where bees visit indiscriminately the differently colored varieties of the same species of flower. *Zinnia elegans* displays white, yellow, orange, red and purple varieties; *Dahlia variabilis* white, yellow, orange, red and purple; and *Centaurea Cyanus* red, white, blue and purple flowers. When visiting any one of these species for nectar bees pass freely from flowers of one color to those of another. Plateau says:

> If in the case of the same plant species the varieties of distinct color are in equal quantities, the insects pass without order from one color to another.[18]

One summer in my garden a single plant of the scarlet runner (*Phaseolus multiflorus*) produced pure white blossoms, which offered a striking contrast to the normal bright scarlet racemes; but honey-bees and bumblebees (*Bombus terricola*) visited both as though they had been of the same hue. Bees likewise ignore the differences of color in the white, rose-red, and purple flowers of *Scabiosa atropurpurea*. But this behavior on the part of bees furnishes no evidence whatever that they can not distinguish colors.

Honey-bees in collecting pollen and nectar are faithful as a rule to a single species of flower—they exhibit "flower fidelity." This is evidently for their advantage, since if they were to pass continually from flowers of one form to those of another much time would be lost in locating the nectar. Even whole colonies may follow this order. Mr. M. H. Mendleson, of Ventura, California, one of the largest honey-producers on the Pacific coast, relates that

> In 1884, one colony out of 200 gathered exclusively from an abundance of mustard bloom; the 199 gathered from the sages.[19]

---

[17] Peckham, George W., and Elizabeth, "Wasps Social and Solitary," p. 6, 1905.

[18] Plateau, F., "Les Insectes et la couleur des fleurs," *L'Année psychologique*, 13, 78.

[19] Mendleson, M. H., *Gleanings in Bee Culture*, October 1, 1908, 36, 1204.

But if the species are closely allied in form and color, as among the buttercups, spiræas and golden-rods, the bees do not carefully discriminate between them. Yet even in these genera the honey-bee often exhibits a remarkable power of distinguishing between allied species, even when they are of the same color. I have described in the AMERICAN NATURALIST how in an upland pasture honey-bees showed a marked preference for the flat-topped corymbs of *Solidago lanceolata* (*Euthamia graminifolia*) to the panicled inflorescence of *S. rugosa.*

> They were repeatedly seen to leave *S. lanceolata,* and after flying about but not resting on the flowers of *S. rugosa* return to the plants they had left only a few moments before. In another instance a bee was seen to wind its way among the plants of the latter species until it found an isolated plant of *S. lanceolata.* A plant of each of the above species was bent over so that the blossoms were intermingled, appearing as a single cluster; a honey-bee rested on *S. lanceolata* and it seemed very probable that it would pass over to the flowers of *S. rugosa,* but such was not the case, for presently it flew away to another plant of the former.[20]

The bees must, therefore, have perceived differences between these two species of *Solidago,* though they occasionally ignored them.

When a plant species displays variously colored flowers, it is obvious that they are alike in shape, odor and nectar, and differ in color alone. Under these circumstances it is for the advantage of bees to pass from one color to another, and this they speedily learn to do. In an earlier paper I have pointed out that form is a more important factor than color in determining the visits of the long-tongued bees and butterflies.[21] This conclusion is confirmed by Dr. Graenicher in a very important contribution on the pollination of the Compositæ. After a careful comparison of the effect of tube length, color, and odor on the limitation of visitors, he says:

> It may be stated that according to the results obtained from a study

---

[20] Lovell, John H., "The Colors of Northern Gamopetalous Flowers," AM. NAT., 37, 453, July, 1903.

[21] Lovell, John H., "The Colors of Northern Gamopetalous Flowers," AM. NAT., 37, 452 and 477–8, July, 1903.

of our Compositæ the proportion of short-tongued to long-tongued visitors in these flowers is determined by tube length more than by any other character of the flower.[22]

In the flowers under consideration the important barrier of difference in form is absent.

In the following experiment it is shown how a bee soon learns to visit colors indiscriminately. On September 22 after a black bee had been accustomed to visit a slip of blue paper, a series of seven differently colored slides were arranged in the following order: black, green, blue, purple, red, white, yellow, orange. The slides were three inches apart, or twenty-two inches from end to end; and there was a small quantity of honey on the center of each. The bee returned the first time to the blue, the second time to the purple, the third time to the purple, the fourth time to the blue, the fifth time to the purple. It will be observed that the bee ceased at once to discriminate between the blue and the purple—the two slides being adjacent and allied in color. On its fifth visit before alighting the bee hovered over the different colors for many seconds, and later left the purple for the red, whence after a brief stop it flew away to the hive.

During the next three visits the bee devoted much time to the examination of the slides, but subsequently it paid little attention to the colors. When the bee returned from the hive, it flew about for a long time, touched on the orange, but immediately left it and went to the blue. On its seventh visit the bee after describing a few circles in the air, touched on the red, then on the blue, went back to the red, and finally stopped on the blue. The colors were arranged in the following order: black, red, blue, white, green, orange, purple, yellow. On its eighth journey before alighting the bee flew from the vicinity of the blue over to the yellow and back to the blue where it remained. There could be no doubt that it was examining the slides, as it flew close to them touching them at times.

I transposed the blue and green slides so that the order was black, green, white, blue, orange, purple, yellow. On its ninth visit the bee returned to the red; on the tenth to the green, then going to red and white, but finally coming back to the green. On its eleventh and twelfth visits the bee returned to the blue. I transposed the blue with the yellow and the red with the purple so that the order of the colors was black, purple, green, white, yellow, orange, red, blue. The thirteenth and fourteenth visits were made to the yellow, the fifteenth to the white, the sixteenth and seventeenth to the yellow, the eighteenth and nineteenth to the blue—on the last visit it was disturbed by a wasp and went to the orange. The twentieth visit was to the yellow, the twenty-first to the green, and the twenty-second to the yellow.

---

[22] Graenicher, S., "Wisconsin Flowers and their Pollination—Compositæ," *Bull. Wis. Nat. Hist. Soc.*, 7, 42, April, 1909.

It is evident that at the beginning of this experiment the behavior of the bee was widely different from what it was at its close. Habituated to visit the blue slide, it continued constant to this slide or the allied purple during its earlier visits; though again and again by means of its visual and olfactory senses it examined and compared the other slides, as has been described. Repeated transpositions of the blue paper gradually weakened its fidelity to this color, until at last similarity of form, honey and odor prevailed over dissimilarity of color, and the bee visited the slides indiscriminately. This result might also have been brought about by permitting the bee to remove all the honey from the blue slide, when it would have turned from necessity to one of the other colors. This is no doubt what happens in nature. A bee finds usually in one flower only a portion of its load of nectar, and so is compelled to examine other blossoms, which, if they are alike in form, it will soon visit without order even though they differ in color. If there are a number of bees, their efforts to avoid visiting the same slide or flower will greatly hasten the breaking down of the color barrier. In a location frequented by a few bees for honey I put out the following series of colors: white, blue, green, black, red orange, purple. In a few minutes there was a bee on every color save black and orange, and a little later there was a bee on each of these slides. The total number of bees was twelve.

That bees can by the aid of their sense perceptions draw "simple instinctive inferences" has also been shown experimentally by Forel. In a bed of dahlias of various colors he mounted red, white and blue paper flowers, in each of which was placed a drop of honey. A red, a white flower and a rose-colored piece of paper with a dry dahlia disc were each brought to the attention of a bee. Thenceforth these three bees, which were marked on the back with blue, yellow and white paints, returned regularly to the artefacts and no longer visited the dahlias.

> The painted bees entirely of their own accord, undoubtedly through an instinctive inference from analogy, discovered the other artefacts as soon as their attention had been attracted by the honey on one of them, notwithstanding the artefacts were some distance from one another and of different colors. For were not the dahlias, too, which they had previously visited of different colors? . . . It would be a fallacy to conclude from this that they do not distinguish colors.[23]

Conclusions

Bees easily distinguish colors, whether they are artificial (paints, dyes, etc.) or natural ("chlorophyll") colors.

Bees are more strongly influenced by a colored slide than by one without color.

Bees, which have been accustomed to visit a certain color, tend to return to it habitually—they exhibit color fidelity.

But this habit does not become obsessional, since they quickly learn not to discriminate between colors when this is for their advantage.

---

[23] Forel, August, "Ants and Some Other Insects," translated by William Morton Wheeler, p. 27.

SHORTER ARTICLES AND DISCUSSION

THE ARITHMETIC OF THE PRODUCT MOMENT METHOD OF CALCULATING THE COEFFICIENT OF CORRELATION

In view of the increasing application of refined statistical methods to scientific problems of all kinds it seems highly desirable to point out any simplification of arithmetical method which may lighten the necessarily formidable labor of calculation.

The statistical constant which has proved a most powerful tool in many fields of work is the coefficient of correlation. Besides the contingency constant[1], the correlation ratio[2] and the well-known four-fold table and product moment methods, several alternative processes of determining correlation in the case of special data have been suggested.[3] In recent numbers of *Science* Dr. Boas[4] and Professor Pearson[5] have discussed the formulæ to be used in the calculation of r, and in another place I have suggested methods[6] which in some cases materially shorten the labor of calculation.

When the nature of the material permits, the best method of calculating correlation is the product moment one.

As conventionally described in the books,[7] this requires for the calculation of $S(xy)$: (*a*) the writing down on the margin of the correlation table of an assumed mean, V_0, of both the x and the y characters, and the plus and minus deviations of the different grades from these origins; (*b*) the entering in the body of the table of the products of the deviations of the several classes of x and y from their respective assumed means, care being taken to regard sign, (*c*) the summation of the products of the class frequencies of x and y by the first two powers of their deviations from their assumed means; (*d*) the multiplication of the frequencies in the table by the products of the deviation of x and y, and the summation of their products, with regard to signs.

---

[1] Pearson, K., "On Contingency and its Relation to Association and Normal Correlation," Draper's Co. Research Memoirs, Biometric Series, 1, 1904.

[2] Pearson, K., "On the General Theory of Skew Correlation and Nonlinear Regression," *ibid.*, 2, 1905 .

[3] For instance, K. Pearson, "On Further Methods of Determining Correlation," *ibid.*, 4, 1907; K. Pearson, "On a New Method of Determining Correlation," *Biometrika*, Vol. VII, pp. 248–257, 1910; K. Pearson, "On a New Method of Determining Correlation," *Biometrika*, Vol. VII, pp. 96–105, 1909.

[4] Boas, F., "Determination of the Coefficient of Correlation," *Science*, N. S., Vol. XXIX, pp. 823-824, 1909.

[5] Pearson, K., "Determination of the Coefficient of Correlation," *Science*, N. S., Vol. XXX, pp. 23–25, 1909.

[6] Harris, J. Arthur, "A short Method of Calculating the Coefficient of Correlation in the Case of Integral Variates," *Biometrika*, Vol. VII, pp. 214-218, 1910.

[7] Yule, G. U., "On the Theory of Correlation," *Jour. Roy. Stat. Soc.*, Vol. LX, p. 812; Davenport, C. B., "Statistical Methods"; Elderton, W. P., "Frequency Curves and Correlation."

This gives

$$S(x'),\ S(x'^2),\ S(y'),\ S(y'^2),\ S(x')/N = d_x,\ S(x'^2)/N = v_2',$$
$$S(y')/N = d_y,\ S(y'^2) = v_2',\ \text{and}\ S(x'y'),$$

from which we may obtain the moments and the products moments about their true means by the use of the formulæ:

$$\sigma_x = \sqrt{v_2' - d_x^2},$$
$$\sigma_{y'} = \sqrt{v_2' - d_y^2},$$
$$S(xy) = S(x'y') - N d_x d_y,$$
$$r = S(xy) / N\sigma_x\sigma_y.$$

Frequently there are several possible ways of carrying out the arithmetic for a given formula, and the one chosen is largely dependent on the mental and mechanical traits of the computer. Personally I have found the process described rather cumbersome, and in using it—especially through the hands of assistants—have found slips coming into the work with unfortunate frequency.

The chief difficulty lies in the fact that the products of the deviations of x and y from their assumed means must be written down as indices to the frequencies in the body of the table itself. This requires considerable time if the table be at all large, and there is no way of checking the results for blunders except to go over the entire process again. After this has been done, all the multiplications of the frequencies into their indices must be carried out and the products summed. If the ranges of variation be at all large, say even no higher than 20 classes each, one may have to multiply some frequencies by such products as 63, 64, 72, 81, etc., and the labor becomes rather great.

Now since the formulæ given above enable us to refer the moments or the product moments taken about any arbitrary point or origin to the true means, I have found the following method to result in a material saving of time and energy.

If for y arrays of integral variates[8] we take 0 instead of the grade thought to be nearest the mean as the origin, we at once obtain the total for the array by summing the products of the frequencies by their grades. By multiplying up by the grade of x character we at once obtain $S(x'y')$.

I illustrate by a table showing the relationship between the number of ovules formed and the number of seeds developing per locule for a series of pods of *Hibiscus Syriacus* taken in the Missouri Botanical Garden in the autumn of 1907. Table I gives the data.

TABLE I

	0	1	2	3	4	5	6	7	8	9	Total.
3	1	1	1	—	—	—	—	—	—	—	3
4	12	12	21	17	5	—	—	—	—	—	67
5	63	115	127	146	153	83	—	—	—	—	687
6	732	1,148	1,415	1,598	1,865	1,829	1,212	—	—	—	9,799
7	208	350	450	525	635	690	714	433	—	—	4,005
8	112	208	300	244	326	368	395	255	151	—	2,359
9	1	5	5	5	2	5	3	9	5	5	45
Total	1,129	1,839	2,319	2,535	2,986	2,975	2,324	697	156	5	16,965

Ovules per locule $= x$, seeds per locule $= y$

The total number of seeds developing for each ovule-class is found with great ease and rapidity by multiplying the frequencies by the number of seeds per locule and *summing at the same time* on the machine.[9] This gives Table II. By multiplying the totals of seeds by the number of ovules in the locules in which they were produced and summing at the same time we find

TABLE II

Ovule Class.	Frequency.	Total Seeds.
3	3	3
4	67	125
5	687	1,834
6	9,799	32,649
7	4,005	16,130
8	2,359	10,047
9	45	229
Totals	16,965	61,017

$$S(x'y') = 400{,}920.$$

---

[8] The method is applicable to graduated variates as well, since in the process of calculation the centers of the classes are taken as integral.

[9] I use a Brunsviga. A comptmeter will serve well for this.

To complete the calculation of the correlation r_{xy}, we require only A_o, A_s, σ_o, σ_s. Taking the origin at 0 for both of these characters[10] and multiplying and summing at the same time, as we did before, we get:

$$S(x') = 109{,}818, \quad S(x'^2) = 721{,}904,$$

$$S(y') = 61{,}017, \quad S(y'^2) = 284{,}287,$$

$$S(x')/N = 109{,}818/16{,}965 = 6.4732 = A_x,$$

$$S(y')/N = 61{,}017/16{,}965 = 3.5966 = A_y,$$

$$\sigma_x = \sqrt{S(x'^2)/N - A_x^2} = .80629,$$

$$\sigma_y = \sqrt{S(y'^2)/N - A_y^2} = 1.95485,$$

$$r_{xy} = \frac{S(x'y')/N - A_x A_y}{\sigma_x \sigma_y} = .2223.$$

Now I think, notwithstanding these large numbers,[11] there has been a material gain in facility of calculation. The writing down of the indices showing the products of deviation has been entirely avoided. The direct calculation of the totals of arrays is easy, and it is only one short step further to obtain the means of arrays for testing linearity, either by the sensible agreement of empirical and theoretical means, as shown by a graph or by the application of Blakeman's test to $\eta^2 - r^2$. Note also that in the conventional method of obtaining $S(x'y')$ there is no way of checking the work except to go over it independently. In the method here described the larger part of the work of obtaining $S(x'y')$ is at once checked by the fact that the sum of the totals of the y arrays $= S(y')$. The final multiplication and summation is very quickly verified.

There are advantages in the method beyond these indicated by this illustration.

Suppose that one wishes to correlate between a first character and a number of repeated characters and their sum. This sometimes happens in work on fertility. Take as an illustration a table[12] showing the relationship between the length of the fruit and the number of ovules on the two placentæ in the bloodroot,

---

[10] Where the range is great it may pay to use the conventional method in calculating the standard deviations. Of course it is quite immaterial for the method of calculating r suggested here, how the constants of the two variables are deduced.

[11] I have purposely chosen an illustration giving large numbers. The series of observations with which we are dealing here is larger than is generally available in biological work.

[12] Table IV, 1907, *Biometrika*, Vol. VII, p. 335, 1910.

TABLE III

Length.	Number of Fruits.	Total Ovules.	Length.	Number of Fruits.	Total Ovules.
21–23	2	19	45–47	208	3,615
24–26	8	94	48–50	142	2,564
27–29	56	636	51–53	50	965
30–32	162	1,922	54–56	20	442
33–35	336	4,442	57–59	18	458
36–38	366	5,106	60–62	4	119
39–41	318	4,590	63–65	2	64
42–44	308	4,868			
			Total	1,000	29,904

Sanguinaria Canadensis. Table III gives the frequency and the total numbers of ovules produced for each length-class.

$$S(x'y') = 1{,}217{,}367.$$[13]

We now calculate the correlation for the length and ovules per placenta or length and total ovules at pleasure. In the first class we have

$$r = \frac{(1{,}217{,}367/2000) - 39.703 \times 14.952}{6.30704 \times 4.61361} = .517 \pm .016,$$

and in the second

$$r = \frac{(1{,}217{,}367/1000) - 39.703 \times 29.904}{6.30704 \times 9.05447} = .527 \pm .015.$$

Again, a worker may have the means and variabilities for two characters p and q, and wish to obtain the correlation without trouble of preparing a formal table. He simply seriates his cards according to the p character, sums the values of the associated q characters and writes down grades of p and the associated totals in a table like II or III. The remainder of the work is as illustrated above.

Or, finally, in short series r may be very quickly calculated by summing the product of the values of the two characters of the individuals, dividing by the total number, subtracting the product of the two means, and dividing the result by the product of the two standard deviations.

---

[13] This number looks rather formidable, but it is read directly from the Brunsviga and can be verified in two or three minutes. Had we centered the length at class 36–38 and the number of ovules at 20, and worked by the conventional method we should have had to calculate and write on the correlation surface nearly 200 of the products of the deviations of the x and y characters from their assumed means. Some of these are rather large and there is no way of checking the work except to go over it independently. All this is obviated by the method suggested here.

The best illustration I have is from Apstein's[14] work on *Mysis*. Table IV shows the body length in millimeters and the number of eggs and embryos for a series of 52 individuals taken February, 1904, and Table V the same characters for a series of 24 taken at all other times in 1904 and 1905.

TABLE IV				TABLE V	
Length and Eggs.	Length and Eggs.	Length and Eggs.	Length and Eggs.	Length and Eggs.	Length and Eggs.
13–9	16–17	18–23	20–66	12–27	19–25
14–9	16–21	18–24	21–26	14–20	19–26
15–11	16–23	18–35	21–34	14–21	19–35
15–13	17–16	18–36	21–48	14–28	19–51
15–13	17–16	19–26	21–51	15–11	19–77
15–16	17–16	19–40	21–51	15–17	20–16
16–13	17–18	19–45	21–58	15–45	20–27
16–14	17–19	20–30	21–62	16–11	20–47
16–14	17–23	20–39	22–24	17–12	21–43
16–16	17–26	20–48	22–47	17–24	22–15
16–17	17–28	20–49	22–68	18–13	23–36
16–17	18–22	20–51	22–71	18–17	
16–17	18–22	20–58	23–67	18–21	

The range of both characters is large. If one were to prepare a regular correlation table (omitting all unnecessary columns and rows) he would have tables of 341 and 222 compartments for the 52 and 24 observations!

Multiplying out with the help of the first two pages of Bartow's tables for the higher squares, we find for the first series: $S(x') = 946$; $S(x'\ ) = 17{,}516$; $S(y') = 1{,}623$; $S(y'^2) = 67{,}089$; $S(x'y') = 31{,}432$; $N = 52$ whence

$$r = [S(x'y')N - 18.1923 \times 31\ 2115] / (2.4261 \times 17.7768) = .85.$$

For the second series $S(x') = 424$; $S(x'^2) = 7{,}672$; $S(y') = 665$; $S(y'^2) = 24{,}149$; $S(x'y') = 12{,}018$; $N = 24$, whence

$$r = [S(x'y') / N - 17.6667 \times 27.7083] / (2.7487 \times 15.4420 = .26.$$

The professional statistician will note that mathematically there is nothing novel in the methods suggested. But I have found them a great service, and since I have never seen them in use[15] by other calculators it seems worth while to direct attention to them.

---

[14] Apstein, C., "Lebensgeschichte von *Mysis mixta* Lillij," *Wissenschaftliche Meeresuntersuchungen*, Abteilung Kiel, N. F., Bd. IX, s. 241–260, 1906.

I give Apstein's data merely as an illustration of a method of calculation. Not only are the numbers too small for biological conclusions of much value, but the series are more or less heterogeneous, coming as they do from several stations. Apstein's own conclusion from his data is "Dass die Zahl der Embryonen nicht so von Salzgehalt als von Grösse der Mutter abhängig ist."

J. ARTHUR HARRIS.

COLD SPRING HARBOR, L. I.,
August 27.

---

[15] In some respects Hardy's summation method described in detail by Elderton in "Frequency Curves and Correlation" is similar, but I believe that the one here proposed requires less labor.

NOTES AND LITERATURE

SCHLOSSER ON FAYÛM MAMMALS[1]

A Preliminary Notice of Dr. Schlosser's Studies upon the Collections made in the Oligocene of Egypt for the Stuttgart Museum, by Herr Markgraf.—The most interesting points are the much greater variety of Hyracoidea, including both bunodont and bunoselenodont types, and the presence of true Primates, which the author refers quite positively to the Anthropoidea. The fauna is also shown to include Chiroptera and Insectivora, the one order represented by the humerus of a large vampyroid bat, *Vampyravus,* the other by a lower jaw, *Metoldobotes,* compared with the somewhat problematical Proglires.

The Primates are represented by three lower jaws, *Mœripithecus, Parapithecus* and *Propliopithecus,* the two latter sufficiently complete to indicate the dentition, which is typically primate, although in the reviewer's opinion the material is not adequate to prove their reference to the Anthropoidea, still less to assert that the last genus is "not only the ancestor of all the Simiidæ, but probably also of the Hominidæ." If the author had stated that the Oligocene ancestor of man probably had lower teeth like those of *Propliopithecus,* the conclusion might well be accepted. But the corollary of Schlosser's statement is that we have found the Oligocene ancestor of man and that he lived in Africa. The evidence is not adequate to warrant any such conclusions. Dr. Schlosser has perhaps no intention of drawing them. But others will promptly do so, and add a little more to the top-heavy and ill-balanced superstructure of speculation and hypothesis which obscures the little that we really do *know* about the ancestry of man and, to a less extent, what we know of the ancestry of most other animals.

The Hyracoidea are discussed at some length. Besides the more typical Saghatheriidæ of Andrews, with bunoselenodont teeth, Schlosser refers to here as a distinct subfamily, the problematical *Geniohyus* of Andrews and defines three new genera, *Pachyhyrax, Mixohyrax* and *Bunohyrax,* intermediate between the two extremes. Six new species are named, but without hint of description. As the paper is avowedly published in order to secure priority for the results of Dr. Schlosser's studies over the concurrent investigations of other authors, it is unfortunate that other authors, however well disposed, can not accept his species as of this date, without violating the rules of nomenclature.

---

[1] Über einige fossile Säugethiere aus dem Oligocän von Agypten," von Max Schlosser, München, *Zoologischen Anzeiger,* Bd. XXXV., Nr. 15, vom 1 Marz, 1910.

Of more importance than questions of priority is Dr. Schlosser's estimate of the affinities of these Fayûm Hyracoids. They differ widely from modern Hyraces in the general form and proportions of the skull (and are singularly like pigs and anthracotheres—W. D. M.) but agree very nearly in the basicranial foramina and jaw articulation, as also in the general construction of carpus and tarsus; the feet are, however, more specialized (as might be expected in view of the larger size of the animals). They are not directly ancestral to the modern Hyracidæ, but *Pliohyrax* of the Pliocene of Samos is apparently descended from *Saghatherium*.

The author regards the Hyracoidea as having no near relations with any other order except the Condylarthra, and as in certain important features cited they are more primitive than any known Condylarth, the relationship can not be very close even here. He disbelieves in the affinity to *Arsinoitherium* suggested by Andrews, holding that this genus is related to the Amblypoda. Any relationship of the Hyracoidea to the Proboscidea through *Mœritherium* must be limited to a common derivation from Condylarth ancestry. He agrees with Sinclair that the Hyracoids have no real affinity with the South American Toxodonts and Typotheres (which, however, can equally well be derived from Condylarth ancestry—W. D. M.) and protests strongly against the names given by Ameghino to several South American genera indicating Hyracoid affinities which Dr. Schlosser regards as a baseless hypothesis. (But to name a genus in indication of its supposed affinities, often subsequently proved erroneous, is so common a procedure, that it is hardly fair to condemn the Argentine paleontologist for following it. The eight new genera named in this paper are every one of them designated in accord with the author's hypothesis as to their relationship, and several of them at least may turn out to be seriously misleading.—W. D. M.)

Among the Carnivora, two new species of *Apterodon* are mentioned, one of which is adequately described, and the problematic genus *Ptolemaia* Osborn is discussed and considered as a highly specialized offshoot of *Cynohyænodon*. (The teeth of this genus are very peculiar, however, and are more suggestive of

Insectivore or even Tæniodont affinities than of Hyænodont derivation. They certainly can not be derived from those of *Cynohyænodon*.—W. D. M.)

A united scapholunar bone is considered to represent a gigantic undescribed Creodont "vielleicht eine *Palæonictis* oder eine *Pachyæna*." (It does not appear, however, why Dr. Schlosser should suggest the presence of these genera. In *Pachyæna* the scaphoid and lunar were certainly separate, nor is there any evidence nor probability that they were united in *Palæonictis;* both genera are of Lower Eocene age, and belong to families of Creodonta of which no trace has been found in the Fayûm fauna or in the Oligocene epoch, and in which the scaphoid and lunar were never united, so far as we know; on the other hand, we know that the Hyænodonts were represented by several genera in the Fayûm and are the only Carnivora positively known in this fauna; they are the only family of Creodonts known to survive into the Oligocene, and in *Hyænodon,* at least, the scaphoid and lunar were sometimes united. The probabilities, therefore, are greatly in favor of this scapholunar representing a large Hyænodont.—W. D. M.)

The presence of Chiroptera in the fauna is an interesting positive addition. The same degree of certainty does not attach to the Insectivora, since the Proglires with which *Metoldobotes* is compared are a group of somewhat doubtful boundaries and affinities. If the Fayûm genus is really related to *Olbodotes* Osborn ("*Oldobotes,*" Schlosser) it is a point of some interest. *Olbodotes* and the almost identical *Mixodectes* form a characteristic group of the Basal Eocene fauna of North America. As Osborn has repeatedly insisted, this fauna was not the source of the later Eocene faunæ in North America, except for a few groups like the Phenacodonts, Coryphodonts and Uintatheres, which gradually disappeared through the course of the Eocene. There is strong support for the hypothesis that it *was* the source of the early Tertiary faunæ of South America which developed in isolation along lines partly parallel with the development of the great Holarctic fauna. The autochthonic element of the early Tertiary fauna of Africa may be derived in a corresponding manner, except that the isolation was not so prolonged or else not so complete. The Cernaysian and Puerco-Torrejon faunæ as known appear to be parts of the same regional fauna, the Paleocene Holarctic. The derivation of Hyracoids, Arsinoitheres, Proboscidea, etc., from this fauna is conjectural because we have no intermediate stages. But the discovery of less progressive and specialized descendants of Paleocene Holarctic animals in the African Oligocene would lend support to this conjecture. Unfortunately, *Metoldobotes* is referable to a group of disputed affinities in which the dentition is a treacherous and uncertain guide, the reviewer feels obliged to accept the reference with reserve; but it is well to point out its significance if confirmed.

The rodent genera described by Osborn are regarded by Schlosser as obviously related to *Theridomys* and *Trechomys* of the European Eocene and Oligocene, the relationship being confirmed by the discovery of an upper jaw. (Osborn compared the originals with specimens of these and other European genera, mostly identified by Dr. Schlosser, expecting to find the affinities close; but the most that the evidence warrants is that they probably belong to the same family. There are genera of several other families of rodents which approach the Theridomyid pattern and dentition as closely as do *Phiomys* and *Metaphiomys* of the Fayûm.)

The foregoing review may appear perhaps unduly critical. But there is an increasing tendency in scientific work towards an uncritical acceptance of the views and conclusions set forth in the work of special research. It becomes peculiarly incumbent, therefore, on those who are engaged in such work to avoid over-positive statements or conclusions based upon inadequate evidence.

Conservative statement and open-mindedness are essential to the permanence of scientific theory. And from Dr. Schlosser, who is justly regarded as one of the greatest living authorities upon Tertiary mammals, we may fairly demand an exceptional degree of conservatism. W. D. MATTHEW.

AMERICAN MUSEUM OF NATURAL HISTORY.

THE OPHIDIAN GENUS GRAYIA

Dr. C. B. Davenport,[1] writing on the imperfection of dominance, has recently remarked that "the weakened character may be retarded in development so that it fails to appear at the normal period but develops later. Thus Lang found hybrids between red and non-red snails to be at first non-red but finally red.[2] Some authors have spoken of this as *reversal of domi-*

[1] *American Breeders' Magazine*, Vol. 1, p. 40.

[2] *Helix nemoralis* var. *libellulo-rubella*; cf. Taylor, "Monog. L. & F. W. Moll. British Is.," part 17, p. 304.

nance, and even Bateson uses this terminology in his latest book. But this is obviously an unfortunate term if dominance means the presence of a quality. For, a given quality, that is due to the absence of a factor, like blue iris [of the eye] color, can not be at one time recessive and at another dominant. If a blue iris appears where brown is expected, the clear reason is that brown pigment has merely failed to develop and is potentially present. A similar case occurs in hybrids between albino and some buff birds; the chicks have a pure white down, only later acquiring the black and buff of the adult plumage.''

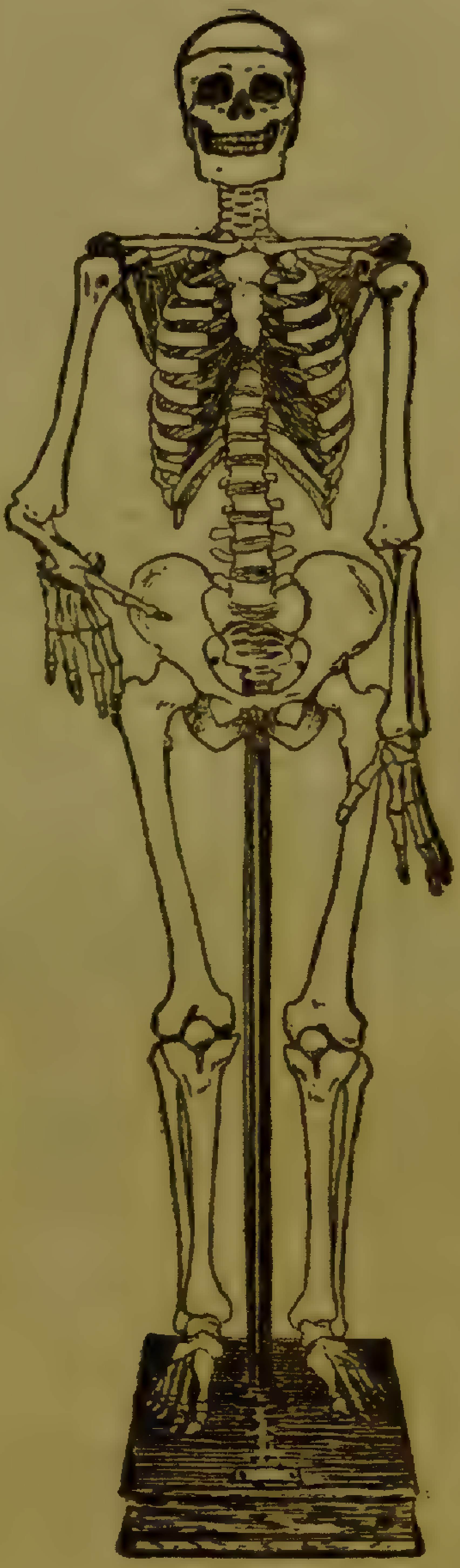
Dr. G. A. Boulenger[3] has recently published a very interesting paper on *Grayia*, a genus of African snakes, in one of which the pattern of the young appears to be completely reversed in the adult. In the young of *Grayia ornata* (Bocage) var. *furcata* (Mocquard) the body is black, with broad whitish or greyish cross-bands, which bifurcate below on each side, so that in lateral view the snake is ornamented with a series of reversed Y's Each Y is slightly speckled with black about the middle line. As the animal grows, the black ground-color gradually changes to grey or brown, owing I suppose to the increase in size without any corresponding increase in pigment-production. The Y's, on the other hand, show more and more black, until they have only a light edge, while in the adult even this disappears, and we have then a series of perfectly *black* markings on a grey ground, in place of similar *light* markings on a black ground. This case is curiously suggestive of those cited by Dr. Davenport, and also interesting as showing that the black markings of the adult are not simply superimposed over the grey or brown, but occupy an area which, but for the black would be pale. This reminds one of the case of the English poppy, which has black spots on red petals, but when the black drops out, as in the Shirley variety, *white* spots appear. The condition found in the snake can hardly be explained by the simple proposition that the animals are heterozygous for the color of the markings, the black being dominant. In this case, we ought apparently to find a certain proportion of recessives, which would retain light Y's to the last. Possibly such occur, but have not been recorded. It seems more likely, however, that tardy development of a pure character here simulates the behavior frequently found in crosses. Incidentally, we may note also the suggestiveness of the case in relation to the development of ocelli.

T. D. A. COCKERELL.

[3] *Proc. Zoological Soc. London,* 1909, pp. 944–952.

The Anatomical Laboratory of Charles H. Ward

189 West Avenue, Rochester, N. Y.



OUR HUMAN SKELETONS are selected specimens scientifically prepared and mounted. They are undoubtedly the finest and strongest skeletons obtainable, and are purchased by the leading Medical and Literary Colleges, Schools, Surgeons, etc. We make a number of special skeletons for demonstrating dislocations, muscular areas, anthropometric landmarks, muscles, etc.

The mounting of the articulations permits movements as in life. Strength and rigidity are secured by the use of a special bronze wire of enormous tensile strength and great resistance to oxidation. Portability and ease of demonstration are attained by our nickeled steel clutch standard, which is a great protection as well.

These skeletons are shipped entirely set up, carefully wrapped, and with detailed directions for unpacking and handling. Our Catalogue gives further details.

OUR SKELETONS OF TYPES OF VERTEBRATES are large specimens, principally of American species, mounted in characteristic poses on polished mahogany pedestals, with nickel-plated brass standards. We offer a type collection for schools and colleges.

ANATOMICAL MODELS

Besides importing duty free for educational institutions we manufacture anatomical models in great variety. These have been purchased by many Schools and Universities. The series includes complete torso, head, brain, nervous system, greatly enlarged models of the sense organs, etc., of most of which we have large half tones. These models pay no duty, no transportation, no middlemen's profits, but are sold direct, at very moderate prices, and can be supplied **promptly when needed.**

We also make **BIOLOGICAL MODELS** of the forms commonly dissected in the laboratory. These models represent complete dissections of the various animals, greatly enlarged (frog 18 inches long, etc.), mounted upon ebonized pedestals, with detailed descriptive labels. Series includes Coral, Sponge, Medusa, Starfish, Diatoma, Leech, Earthworm, Clam, Crayfish, Amphioxus, Perch, Frog. Sample labels and halftones on request.

ANTHROPOLOGY AND ETHNOLOGY

The Finsch Life Masks of Aborigines, including those islanders recently acquired by the United States. Casts of Skulls, Skeletons and Brain, of Prehistoric Man. Casts of prehistoric bone carvings from the caves of France. Stone implements of the North American Indians.

RELIEF MAPS OF THE UNITED STATES, the Continents, Grand Cañon of the Colorado, Yosemite Valley, etc., made in Washington, D. C., for the United States Geological Survey and others by Howell (a former member of the Survey). **The only authoritative relief maps made commercially in America.** They are light, strong (made of papier maché), beautifully colored and lettered, and as low in price as "cheap" maps. For catalogues, halftones of models, maps, etc., address

CHARLES H. WARD

189 West Avenue, Rochester, N. Y.

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE MAY NUMBER

A Review of Some Recent Criticisms of the Restorations of Sauropod Dinasaurs. DR. J. W. HOLLAND.

Anatomical Characters in the Evolution of Pinus. IRVING W. BAILEY.

Facts about the "Lobster Pearl." Professor FRANCIS H. HERRICK.

Shorter Articles and Discussion: An Eighteenth Century Microscope, Professor BASHFORD DEAN. Stomatolepas, a Barnacle Commensal in the Throat of the Loggerhead Turtle. HENRY A. PILSBRY. The Age of Speed Sires, CASPER L. REDFIELD.

Notes and Literature: *Biometrics*—Recent Quantitative Studies in Variation in Social Insects, DR. RAYMOND PEARL. *Experimental Zoology*—The Effects of Extirpation and of Transplantation of the Reproductive Organs in Insects, E. N. BROWNE. Wheeler on Ants, Professor G. H. PARKER.

CONTENTS OF THE JUNE NUMBER

The Botanical Society of America: The Nature of Physiological Response. The Late Professor CHARLES R. BARNES.

The Place of Plant Responses in the Categories of Sensitive Reactions. Professor FREDERICK C. NEWCOMBE.

The Larva and Spat of the Canadian Oyster. Dr. J. SAFFORD.

The Alimentary Canal of a Carboniferous Salamander. Dr. ROY L. MOODIE.

Shorter Articles and Discussion: Observations on the Spawning Habits of Hydroides Dianthus. Professor CHARLES W. HARGITT.

Notes and Literature: *Protozoa*—Doflein's Lehrbuch der Protozoenkunde: Professor CHARLES A. KOFOID. Celebrating Darwin's Greatness and Darwinism's Weakness, V. L. K.

CONTENTS OF THE JULY NUMBER

A Consideration of the "Species Plantarum" of Linnaeus as a Basis for the Starting Point of the Nomenclature of Cryptogams. Professor W. G. FARLOW.

Notes on Some Beaufort Fishes. E. W. GUDGER.

On the Effect of External Conditions on the Reproduction of Daphnia. Dr. J. F. MCCLENDON.

Are Fluctuations Inherited? Dr. HARRY H. LOVE.

Inheritance in Potatoes. Professor EDWARD M. EAST.

Shorter Articles and Correspondence: The Age of Speed Sires: Professor F. R. MARSHALL.

Notes and Literature: Russo on Sex-Determination and Artifical Modification of the Mendelian Ratios, Professor W. E. CASTLE; The Bubonic Plague, Professor H. B. WARD; Desert Plants, WILLIAM L. BRAY.

CONTENTS OF THE AUGUST NUMBER

Chromosomes and Heredity. Professor T. H. MORGAN.

Spiegler's "White Melanin" as Related to Dominant or Recessive White. Dr. ROSS AIKEN GORTNER.

Shorter Articles and Correspondence: A Pickwickian Contribution to Our Knowledge of Wasps: Professor KARL PEARSON.

Notes and Literature: Heredity, Dr. W. J. SPILLMAN.

CONTENTS OF THE SEPTEMBER NUMBER

Nuclear Phenomena of Sexual Reproduction in the Algæ. DR. BRADLEY MOORE DAVIS.

Nuclear Phenomena of Sexual Reproduction in Fungi. PROFESSOR R. A. HARPER.

The Pose of the Sauropodous Dinosaurs. DR. W. D. MATTHEW.

Shorter Articles and Discussion: Evolution without Isolation, DR. JOHN T. GULICK. Retroactive Selection, CASPER L. REDFIELD. The Logic of Chance in Problems of Genetics, ARTHUR S. DEWING.

Notes and Literature: Animal Structure and Habits, Professor G. H. PARKER. Plant Physiology, C. L. SHEAR.

CONTENTS OF THE OCTOBER NUMBER

Variations in Urosalpinx. Dr. HERBERT EUGENE WALTER.

Nuclear Phenomena of Sexual Reproduction in Gymnosperms. CHARLES J. CHAMBERLAIN.

Nuclear Phenomena of Sexual Reproduction in Angiosperms. Professor D. M. MOTTIER.

Shorter Articles and Discussion: Sterility, Dr. MAX MORSE.

Notes and Literature: Notes on Ichthyology, President DAVID STARR JORDAN. The Mammals of Colorado, Professor T. D. A. COCKERELL.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

VOL. XLIV, NO. 528 **DECEMBER, 1910**

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. **Heredity of Skin Pigmentation in Man.** GERTRUDE C. DAVENPORT and CHARLES B. DAVENPORT - - - - - - - - - - - 705

II. **Spawn and Larva of Ambystoma Jeffersonianum.** Professor W. H. PIERSOL 732

III. **The Inheritance of Sizes and Shapes in Plants.** Professor R. A. EMERSON - 739

IV. **Shorter Articles and Discussion:** The Modification of Mendelian Inheritance by External Conditions. Professor T. D. A. COCKERELL - - - - - 747

V. **Notes and Literature:** Heredity, Dr. W. J. SPILLMAN. - - - - - 750

VI. **Index to Volume XLIV** - - - - - - - - - - - - 753

THE SCIENCE PRESS

LANCASTER, PA. **GARRISON, N. Y.**

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

THE BULLETIN—For bargains in Ethnographical and Pre-historic Specimens. Books on Natural History, Science, Travel, Voyages, etc. See THE BULLETIN post free for 3 cent stamp.

4 Duke St., Adelphi—London—England

NATURE

BOOKS

FRANKLIN BOOKSHOP

S. N. RHOADS, Prop.

920 Walnut St. Philadelphia

Second-hand Books Relating to Natural History.

Write for New Catalog.

Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

Henry Holt & Company

34 West 33d St., New York

378 Wabash Ave., Chicago

Microscopes and Accessories

Hand Cameras of Highest Quality

Binoculars, Prism and Galilean

the best obtainable for Nature Study

Scientific Instruments

Laboratory Apparatus

Max Meyer 18 West 27th St. New York

"Quality, Prices, Service Right."

THE
AMERICAN NATURALIST

VOL. XLIV *December, 1910* No. 528

HEREDITY OF SKIN PIGMENT IN MAN. II

GERTRUDE C. DAVENPORT AND CHARLES B. DAVENPORT

CARNEGIE INSTITUTION OF WASHINGTON, STATION OF EXPERIMENTAL EVOLUTION, COLD SPRING HARBOR, N. Y.

E. INHERITANCE OF ALBINISM

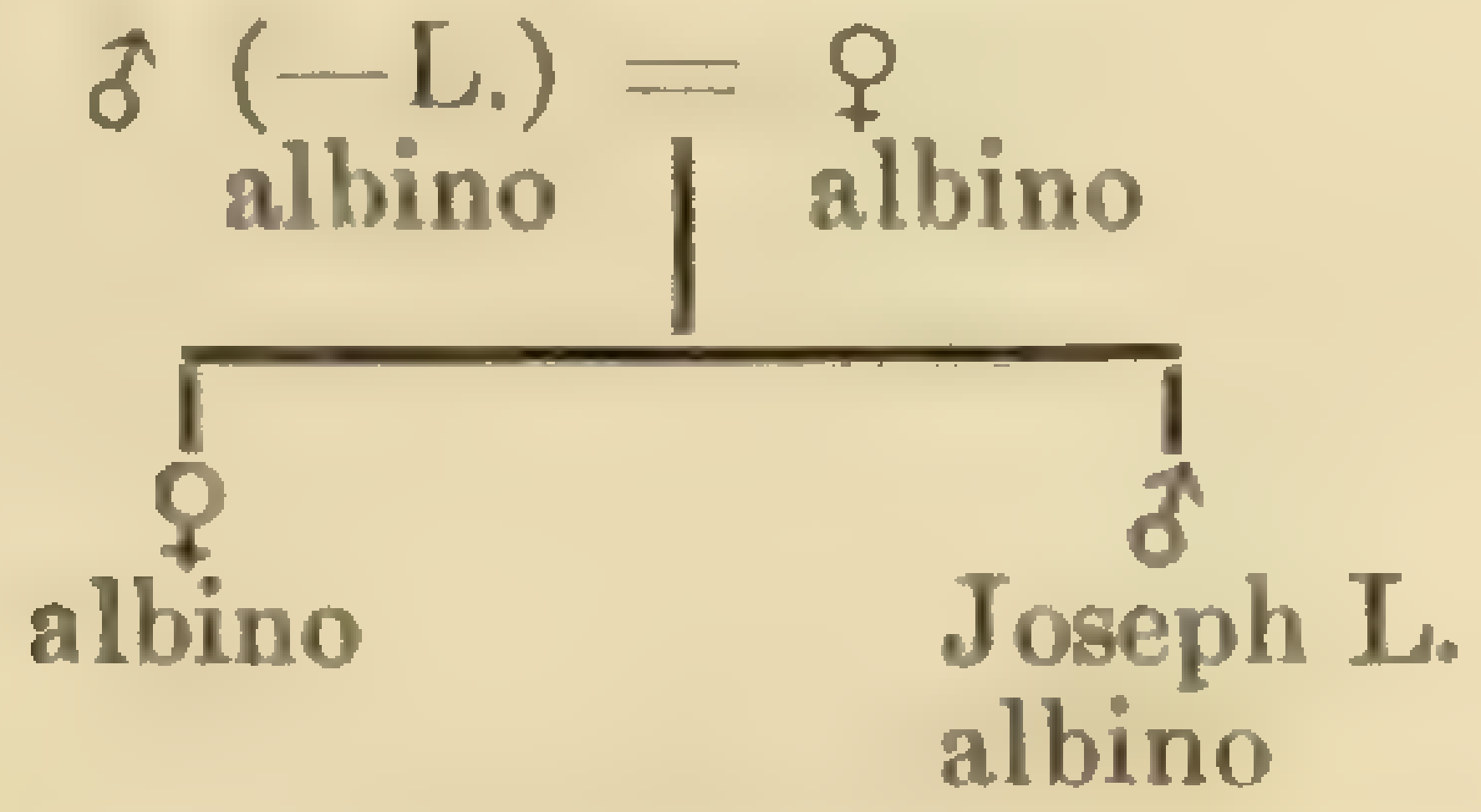
Albinism is the absence of pigmentation through lack of either, or both, the chromogen and the oxidizing ferment. The condition occurs widespread among animals and plants. In man it is rather rare, probably not occurring (if one may hazard a mere guess) in the population of the United States, as a whole, in more than in one case in 10,000 people.

Of true albinism in man there are all degrees. Aside from the piebald condition occasionally found in colored persons there are various grades of uniform depigmentation—hair color varying from light yellow to pure white; irides varying from pale blue to absence of blue, and pupils varying in the intensity of the pink color. Indeed, there is abundant testimony that persons born as albinos may acquire a slight pigmentation. Such a case was cited by Dr. H. B. Young (1905) from Illinois. Albino cats also vary in the pinkish glow of the retina.

Despite variations in the completeness of depigmentation albinism can usually be clearly distinguished, at least in its more marked grades, and so we can study its inheritance. The cases given below were mostly collected by ourselves alone, or with the aid of a medically trained assistant, Dr. Sumner Everingham, and many of the albinos were seen by us.

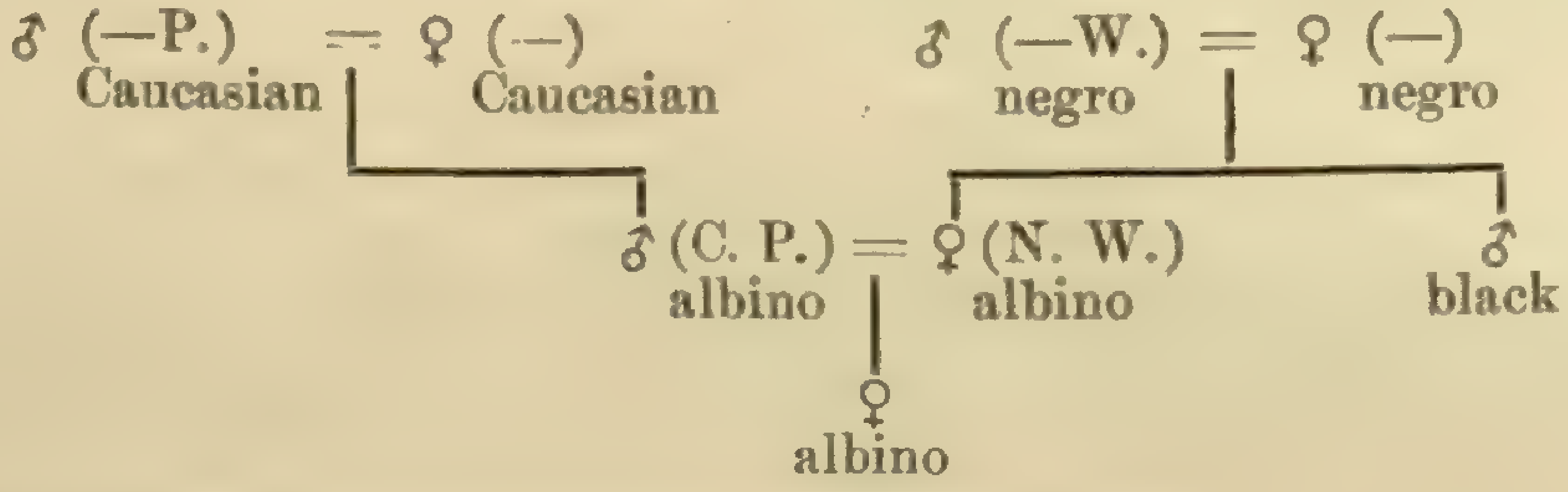
I. Both Parents are Albinos

1. Luc. Family


♂ (—L.) = ♀
albino
albino
♀
albino
♂
Joseph L.
albino

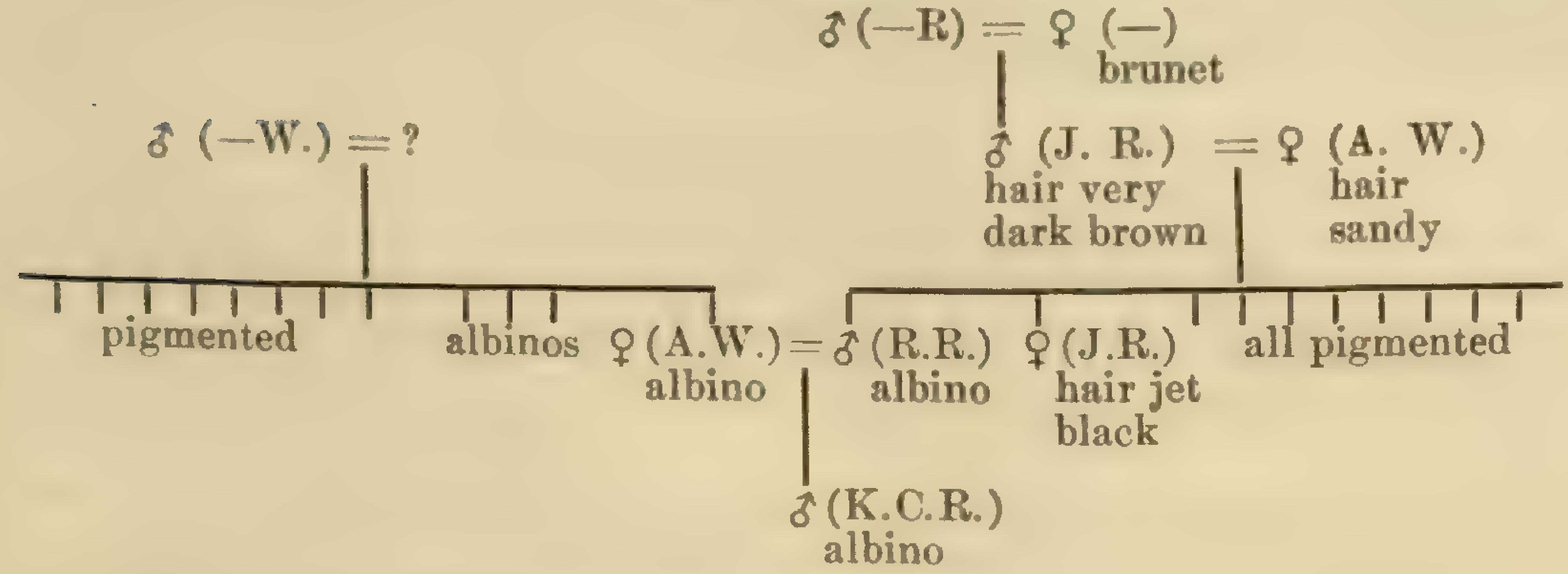
Note.—This case is on the authority of Mr. Rob Roy, an albino who seems entirely trustworthy, and has met many albinos in the "show" business.

2. Pri. Family


♂ (—P.) = ♀ (—)
Caucasian
Caucasian
♂ (—W.) = ♀ (—)
negro
negro
♂ (C. P.) = ♀ (N. W.)
albino
albino
♂
black
♀
albino

Note.—This case also on the authority of Rob Roy.

3. R. Family

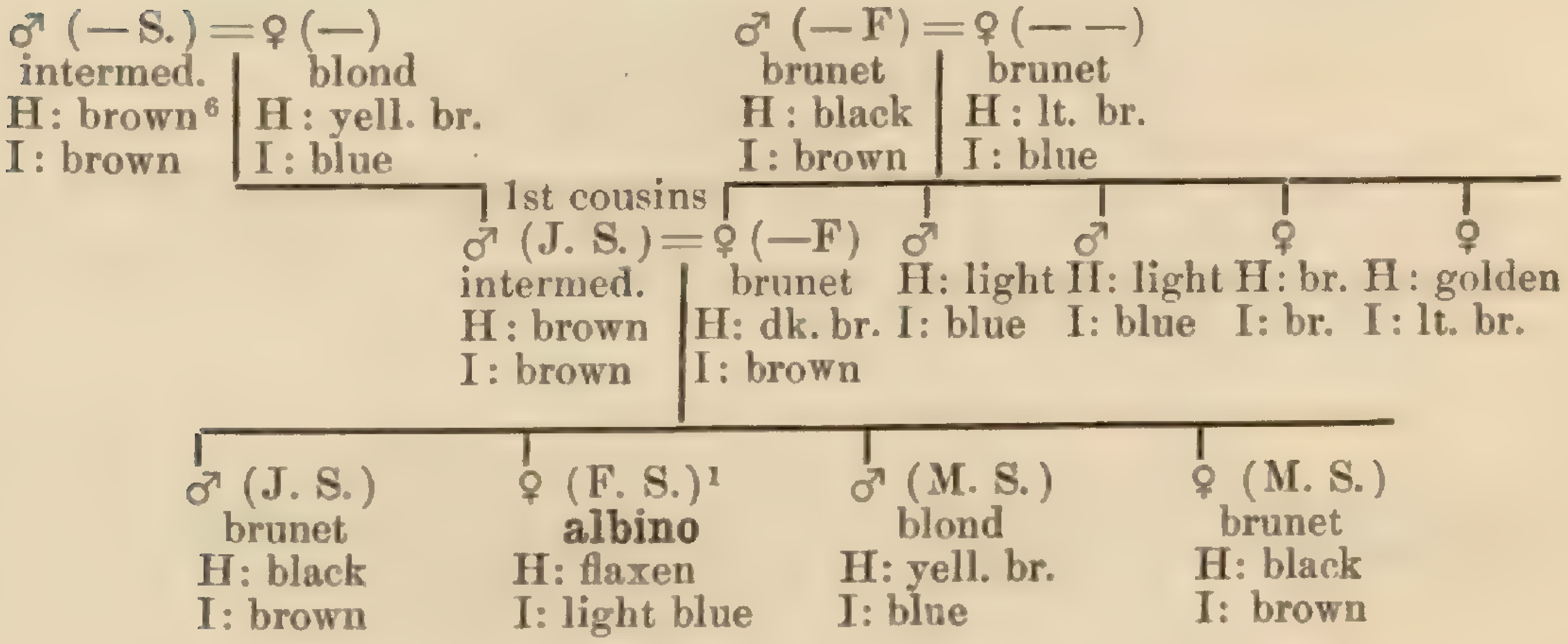

♂ (—R) = ♀ (—)
brunet
♂ (—W.) = ?
♂ (J. R.) = ♀ (A. W.)
hair very dark brown
hair sandy
pigmented
albinos
♀ (A.W.) = ♂ (R.R.)
albino
albino
♀ (J.R.)
hair jet black
all pigmented
♂ (K.C.R.)
albino

Note.—R. R. seen by me.

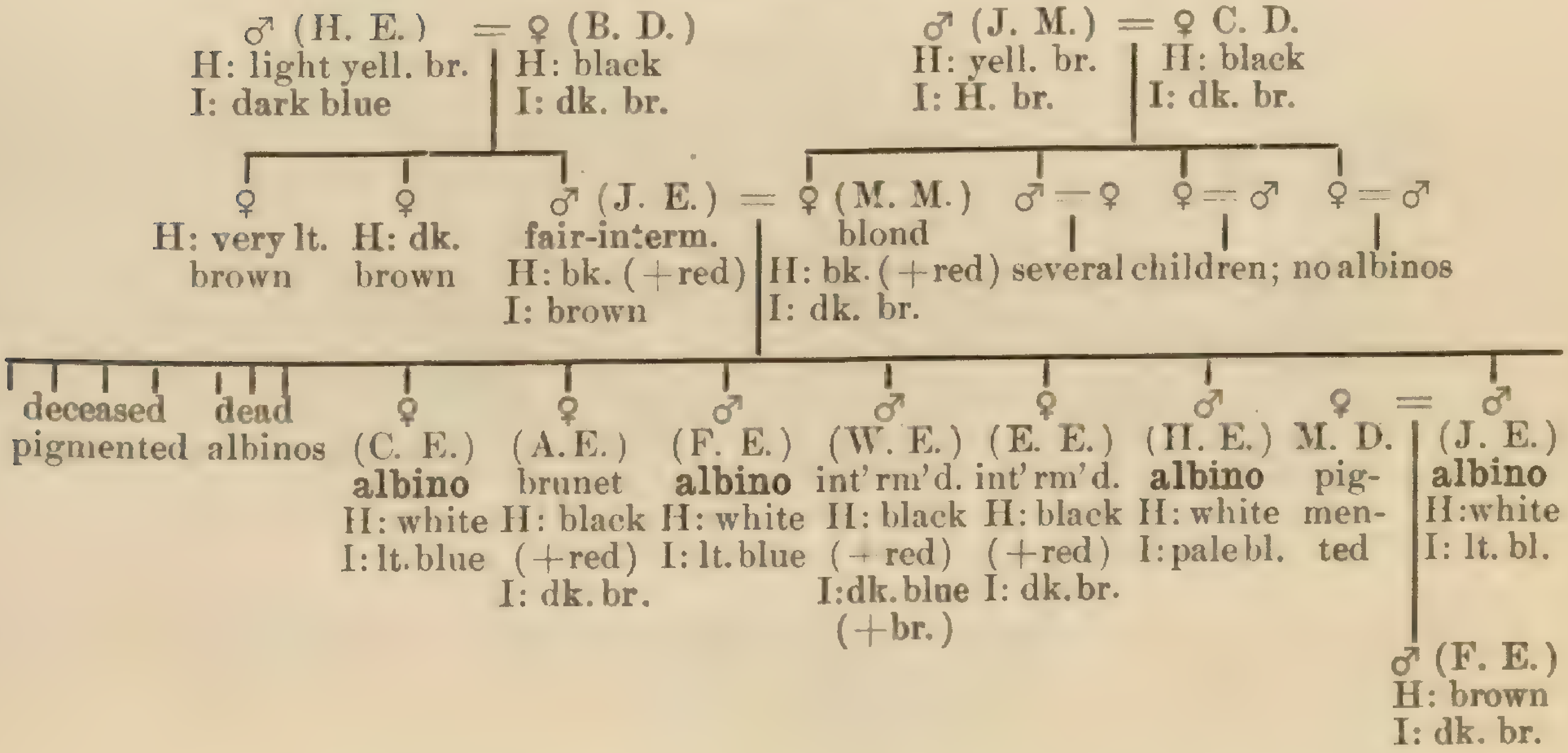
II. NEITHER PARENT ALBINIC

(a) *Albinos in Caucasian Families with Admitted Consanguinity*

4. SHE. FAMILY


♂ (—S.) = ♀ (—)
intermed.
H: brown[6]
I: brown
blond
H: yell. br.
I: blue
♂ (—F) = ♀ (— —)
brunet
H: black
I: brown
brunet
H: lt. br.
I: blue
1st cousins
♂ (J. S.) = ♀ (—F)
intermed.
H: brown
I: brown
brunet
H: dk. br.
I: brown
♂ H: light I: blue
♂ H: light I: blue
♀ H: br. I: br.
♀ H: golden I: lt. br.
♂ (J. S.) brunet H: black I: brown
♀ (F. S.)[1] albino H: flaxen I: light blue
♂ (M. S.) blond H: yell. br. I: blue
♀ (M. S.) brunet H: black I: brown

5. ENN. FAMILY (IRISH ORIGIN)


♂ (H. E.) = ♀ (B. D.)
H: light yell. br.
I: dark blue
H: black
I: dk. br.
♂ (J. M.) = ♀ C. D.
H: yell. br.
I: H. br.
H: black
I: dk. br.
♀ H: very lt. brown
♀ H: dk. brown
♂ (J. E.) = ♀ (M. M.)
fair-interm.
H: bk. (+red)
I: brown
blond
H: bk. (+red)
I: dk. br.
♂ = ♀ ♀ = ♂ ♀ = ♂
several children; no albinos
deceased pigmented
dead albinos
♀ (C. E.) albino H: white I: lt. blue
♀ (A. E.) brunet H: black (+red) I: dk. br.
♂ (F. E.) albino H: white I: lt. blue
♂ (W. E.) int'rm'd. H: black (+red) I: dk. blue (+br.)
♀ (E. E.) int'rm'd. H: black (+red) I: dk. br.
♂ (H. E.) albino H: white I: pale bl.
♀ M. D. pigmented
♂ (J. E.) albino H: white I: lt. bl.
♂ (F. E.) H: brown I: dk. br.

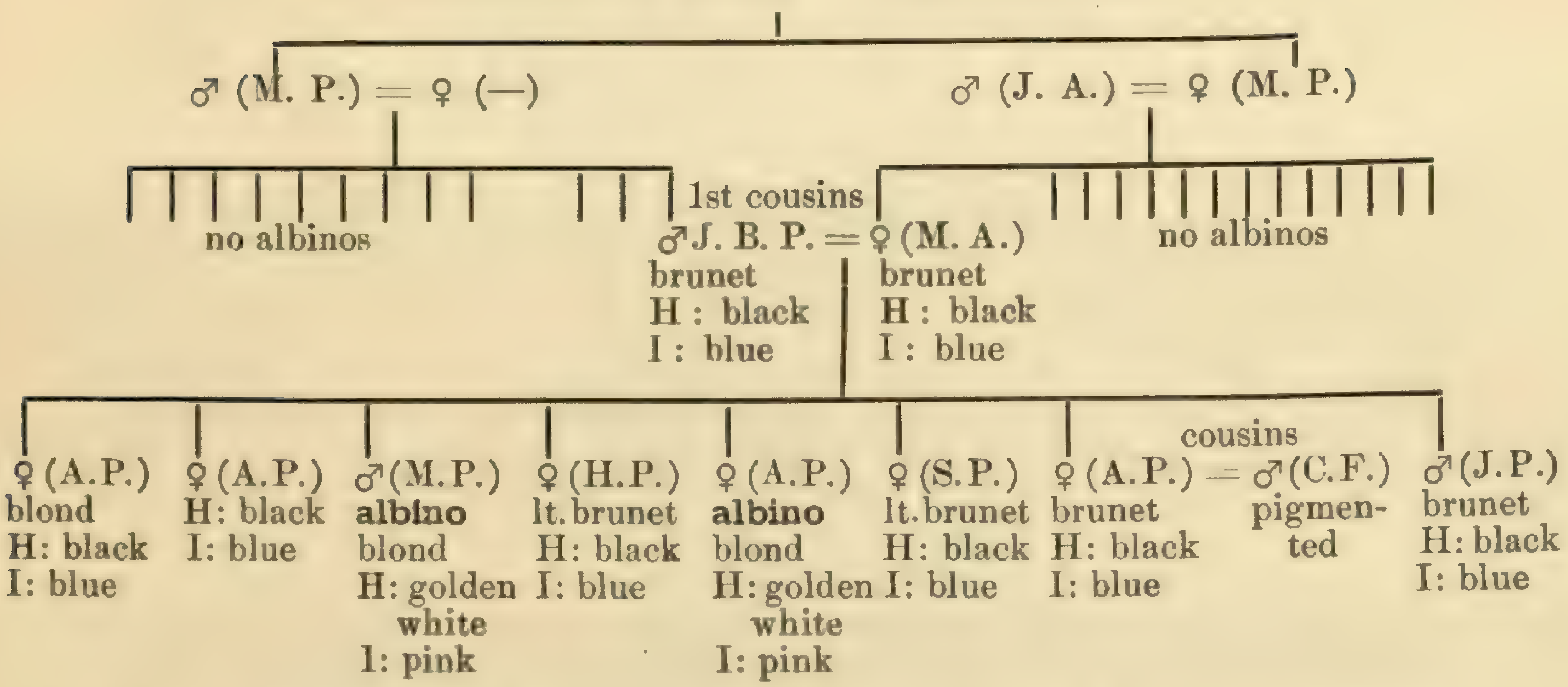
Note.—Three generations known; no other albinos. The father and mother, JE and MM, are distant cousins (not first); and father's mother and mother's mother bear the same surname and come from the same place in Ireland. The youngest son (JE) married a distant cousin having the same surname as both his grandmothers. Seen by C. B. D.

---

[6] In the pedigree tables H indicates hair color; I iris color.

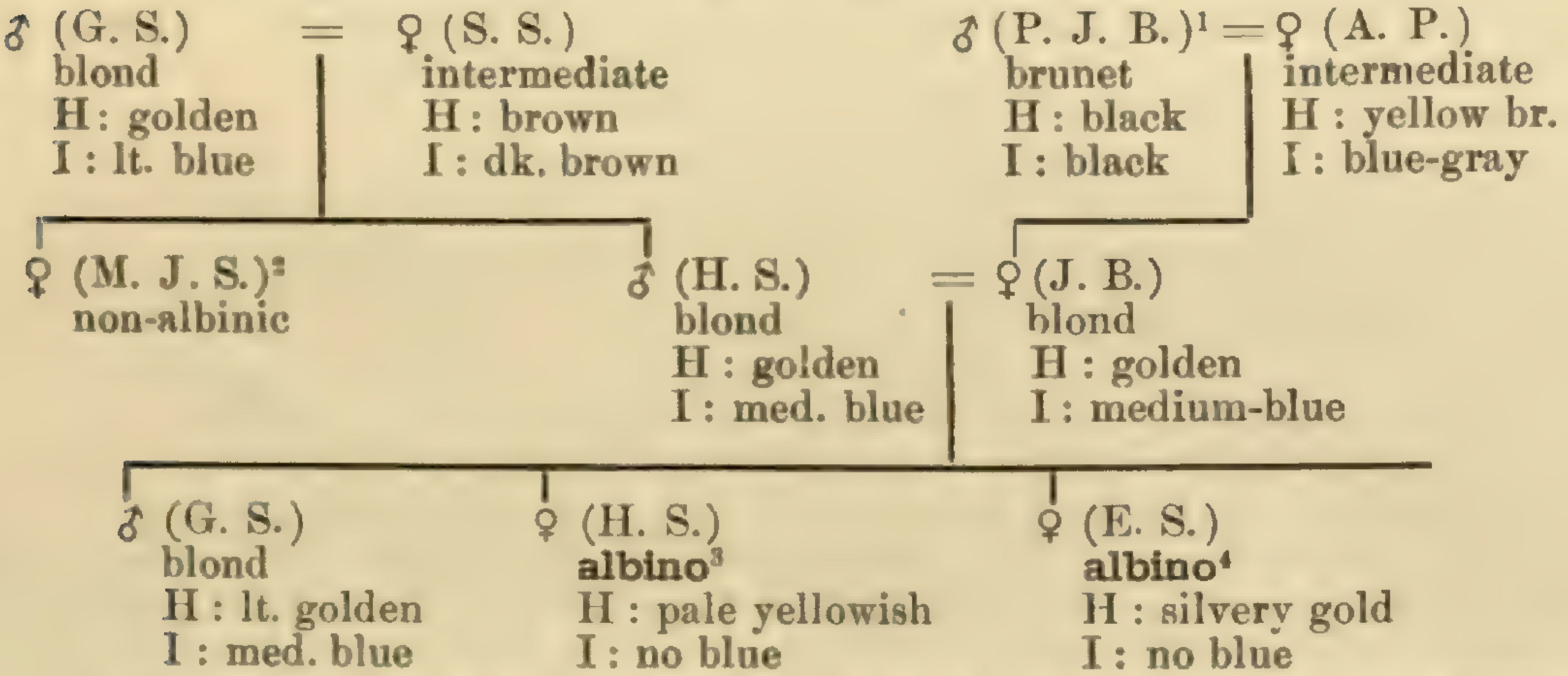
[7] Hair faintly yellowish; irides pale blue; retina, medium pinkish glow; nystagmus moderate; congenital myopia; school work satisfactory; father and mother first cousins. Seen by S. E.

6. PAR. FAMILY


♂ (M. P.) = ♀ (—)
♂ (J. A.) = ♀ (M. P.)
no albinos
1st cousins
♂ J. B. P. = ♀ (M. A.)
no albinos
brunet
H: black
I: blue
brunet
H: black
I: blue
♀ (A.P.)
blond
H: black
I: blue
♀ (A.P.)
H: black
I: blue
♂ (M.P.)
albino
blond
H: golden white
I: pink
♀ (H.P.)
lt. brunet
H: black
I: blue
♀ (A.P.)
albino
blond
H: golden white
I: pink
♀ (S.P.)
lt. brunet
H: black
I: blue
cousins
♀ (A.P.) = ♂ (C.F.)
brunet
H: black
I: blue
pigmented
♂ (J.P.)
brunet
H: black
I: blue

(*b*) *Albinos in Families with Suspected Consanguinity*

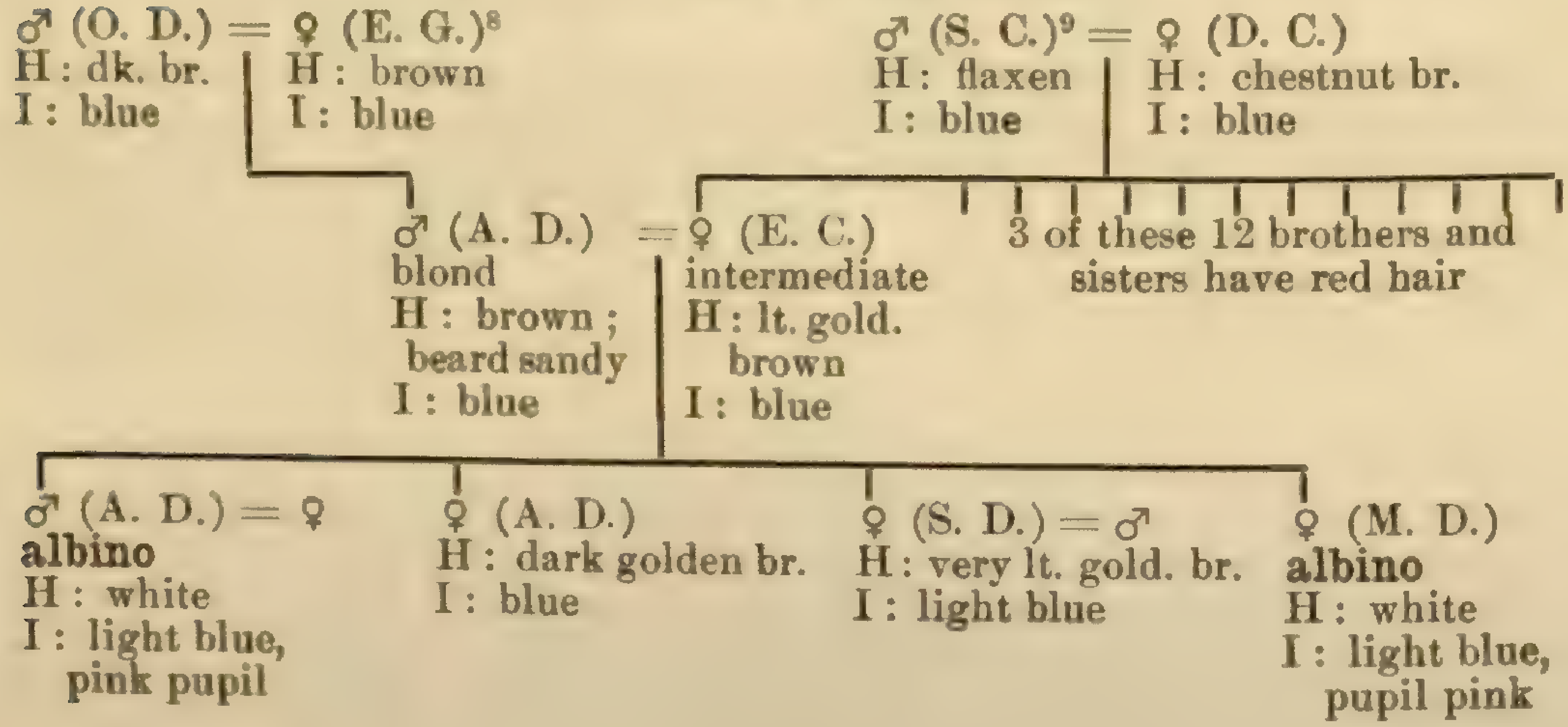
7. SAC. FAMILY


♂ (G. S.)
blond
H: golden
I: lt. blue
♀ (S. S.)
intermediate
H: brown
I: dk. brown
♂ (P. J. B.)¹ = ♀ (A. P.)
brunet
H: black
I: black
intermediate
H: yellow br.
I: blue-gray
♀ (M. J. S.)²
non-albinic
♂ (H. S.)
blond
H: golden
I: med. blue
♀ (J. B.)
blond
H: golden
I: medium-blue
♂ (G. S.)
blond
H: lt. golden
I: med. blue
♀ (H. S.)
albino³
H: pale yellowish
I: no blue
♀ (E. S.)
albino⁴
H: silvery gold
I: no blue

Note.—Seen by C. B. D. and S. E. [1] and [2] have the same middle name. [3] and [4] show reddish glow through pupil.

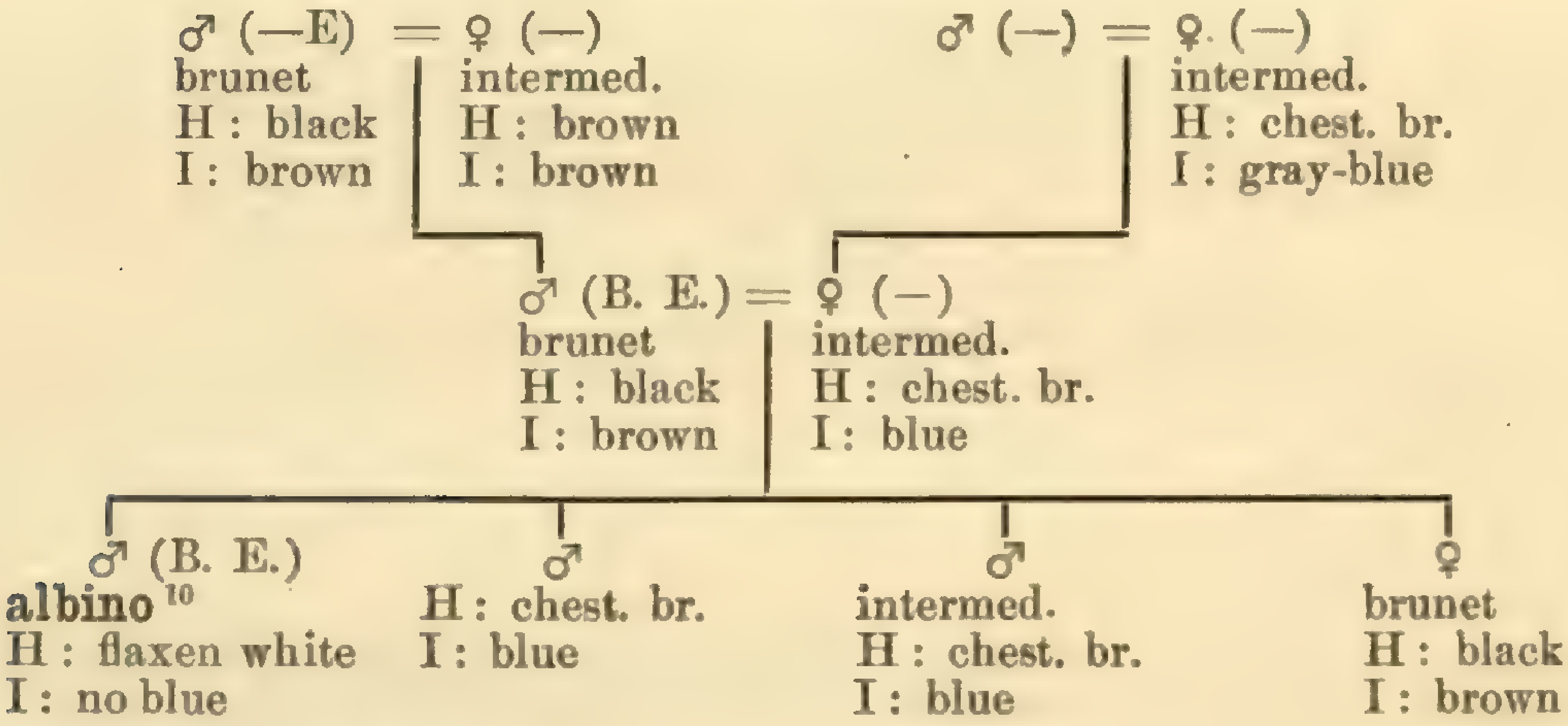
(*c*) *Albinos in Caucasian Families with no Evidence of Consanguinity*

8. DON. FAMILY (IRISH ORIGIN)


♂ (O. D.) = ♀ (E. G.)⁸
H: dk. br.
I: blue
H: brown
I: blue
♂ (S. C.)⁹ = ♀ (D. C.)
H: flaxen
I: blue
H: chestnut br.
I: blue
♂ (A. D.) = ♀ (E. C.)
blond
H: brown; beard sandy
I: blue
intermediate
H: lt. gold. brown
I: blue
3 of these 12 brothers and sisters have red hair
♂ (A. D.) = ♀
albino
H: white
I: light blue, pink pupil
♀ (A. D.)
H: dark golden br.
I: blue
♀ (S. D.) = ♂
H: very lt. gold. br.
I: light blue
♀ (M. D.)
albino
H: white
I: light blue, pupil pink

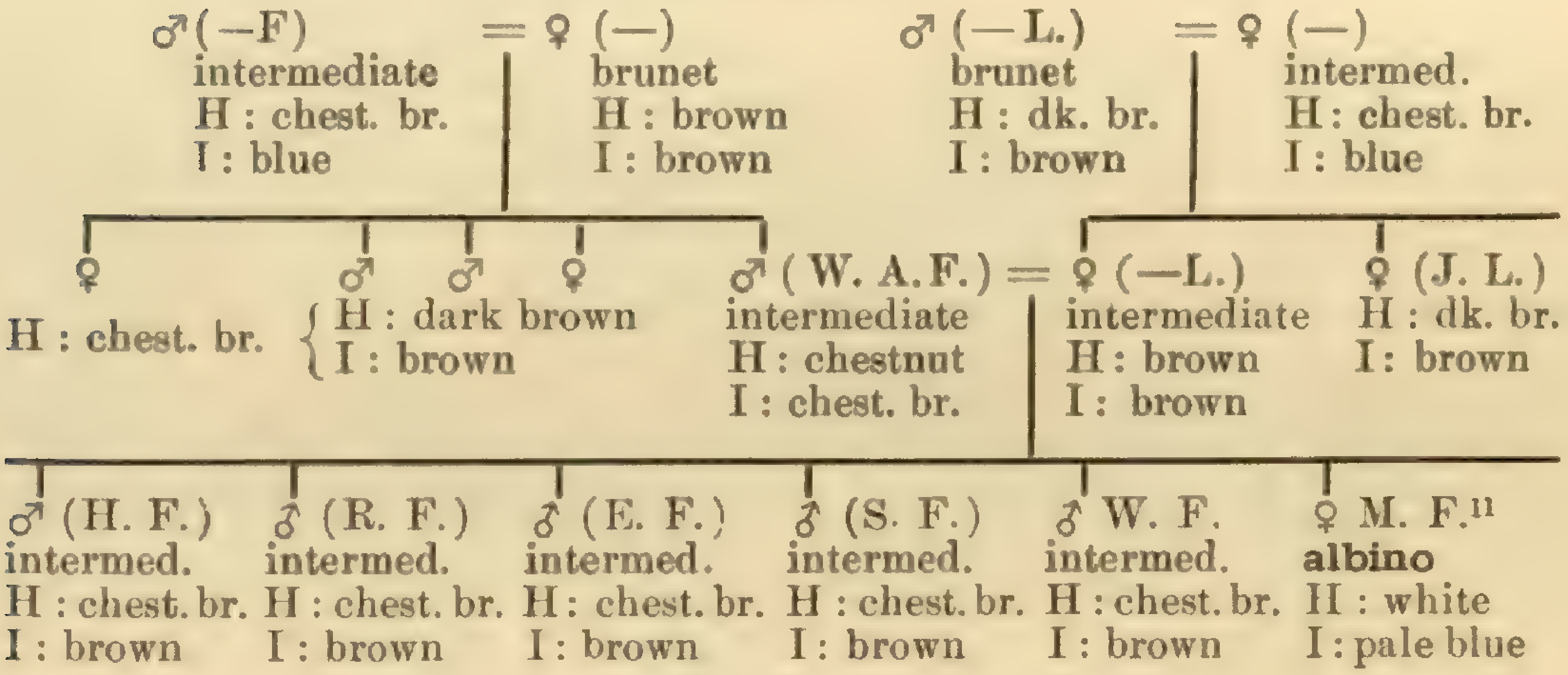
Note.—Seen by C. B. D. No relative on either side known to be an albino.

9. Ed. Family


♂ (—E) = ♀ (—)
brunet
H : black
I : brown
intermed.
H : brown
I : brown
♂ (—) = ♀ (—)
intermed.
H : chest. br.
I : gray-blue
♂ (B. E.) = ♀ (—)
brunet
H : black
I : brown
intermed.
H : chest. br.
I : blue
♂ (B. E.)
albino[10]
H : flaxen white
I : no blue
♂
H : chest. br.
I : blue
♂
intermed.
H : chest. br.
I : blue
♀
brunet
H : black
I : brown

Note.—Seen by S. E.

10. Far. Family


♂ (—F) = ♀ (—)
intermediate
H : chest. br.
I : blue
brunet
H : brown
I : brown
♂ (—L.) = ♀ (—)
brunet
H : dk. br.
I : brown
intermed.
H : chest. br.
I : blue
♀
H : chest. br.
♂ ♂ ♀
H : dark brown
I : brown
♂ (W. A. F.) = ♀ (—L.)
intermediate
H : chestnut
I : chest. br.
intermediate
H : brown
I : brown
♀ (J. L.)
H : dk. br.
I : brown
♂ (H. F.)
intermed.
H : chest. br.
I : brown
♂ (R. F.)
intermed.
H : chest. br.
I : brown
♂ (E. F.)
intermed.
H : chest. br.
I : brown
♂ (S. F.)
intermed.
H : chest. br.
I : brown
♂ W. F.
intermed.
H : chest. br.
I : brown
♀ M. F.[11]
albino
H : white
I : pale blue

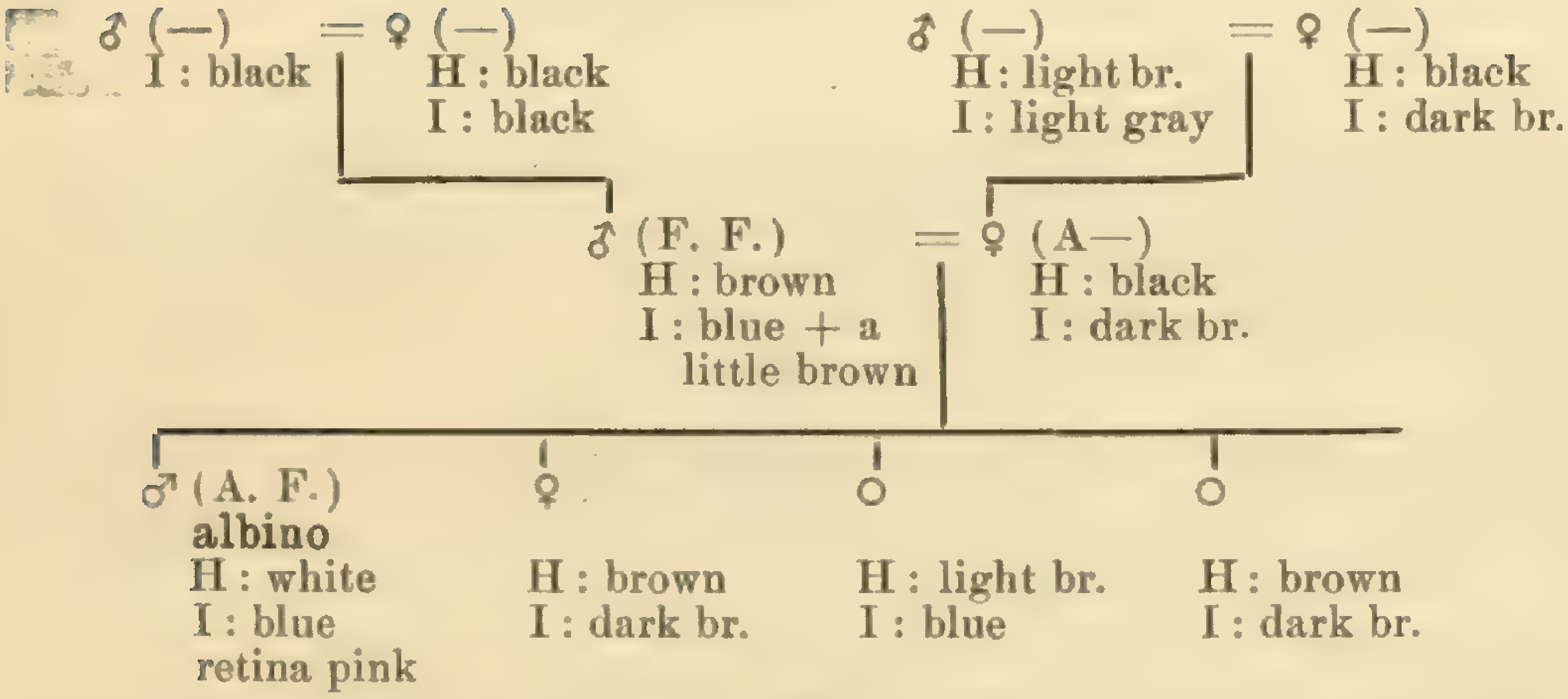
[8] Some relatives with sandy hair.

[9] Many of his relatives have red hair.

[10] Hair white as snow; retina with bright pinkish glow; nystagmus moderate; shortsighted; can read 9 pt. Modern (Roman) type at three inches from eyes; school work middling. Red hair in ancestry, three generations back.

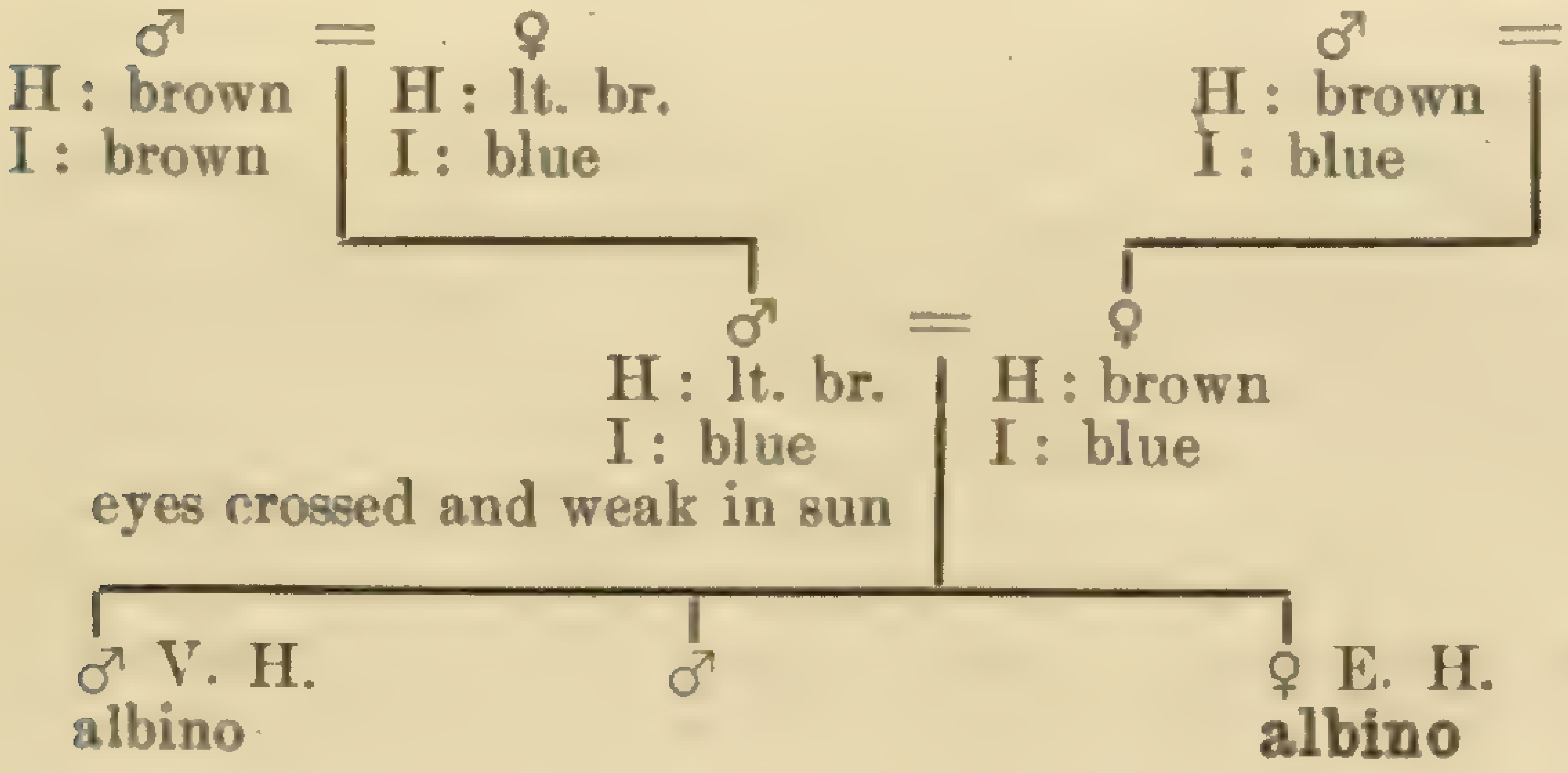
[11] Seen by S. E. Retina, medium pinkish glow; nystagmus slight; reads No. 9 Modern (Roman) print at nine inches; school work satisfactory. No consanguinity known.

11. Fer. Family (Italian)


♂ (—)
I : black
= ♀ (—)
H : black
I : black
♂ (—)
H : light br.
I : light gray
= ♀ (—)
H : black
I : dark br.
♂ (F. F.)
H : brown
I : blue + a little brown
= ♀ (A—)
H : black
I : dark br.
♂ (A. F.)
albino
H : white
I : blue
retina pink
♀
H : brown
I : dark br.
○
H : light br.
I : blue
○
H : brown
I : dark br.

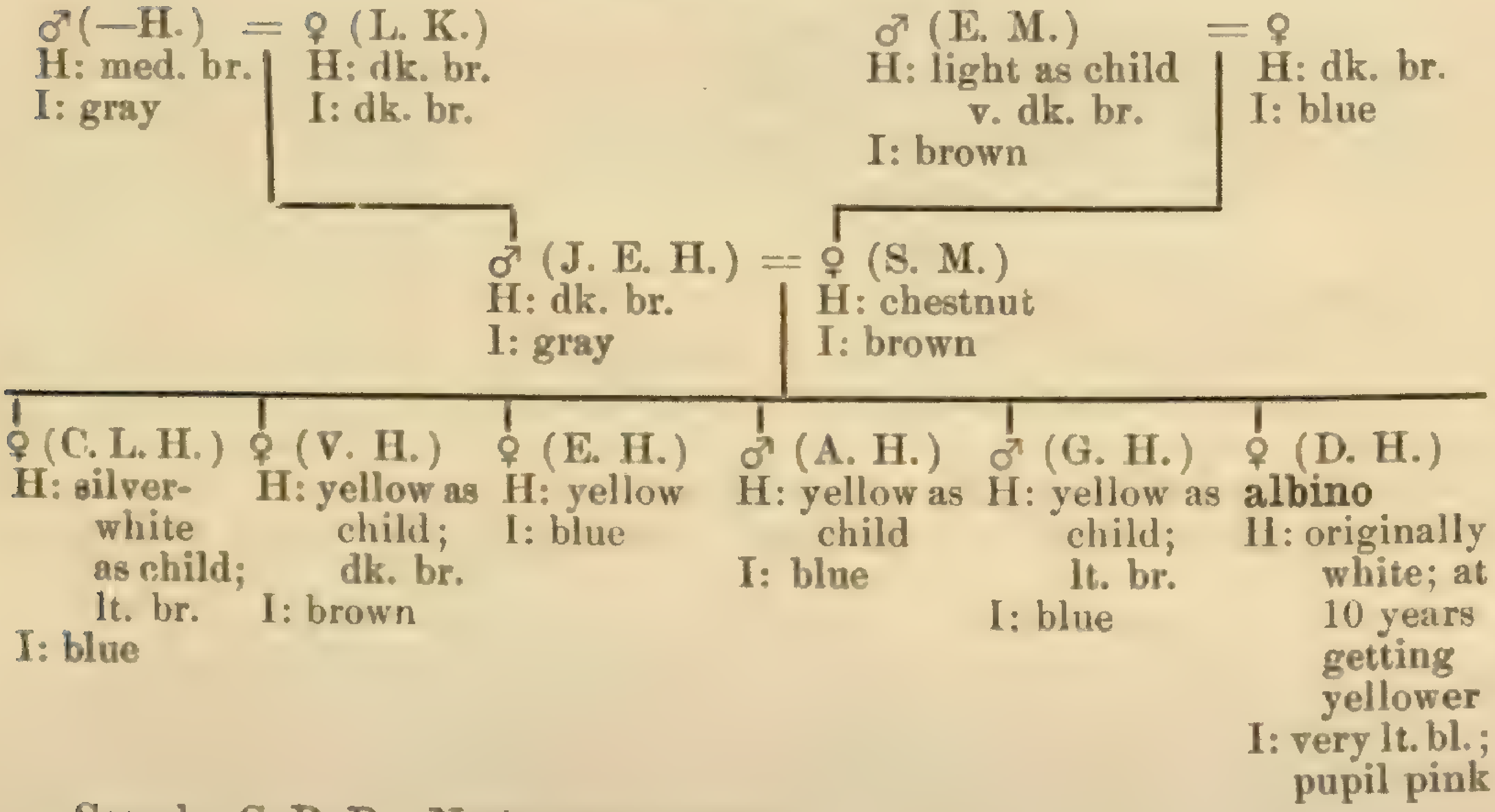
Note.—Seen by C. B. D. No consanguinity so far as known. No other albino relatives recalled.

11a. Hlo. Family (Bohemian)


♂
H : brown
I : brown
= ♀
H : lt. br.
I : blue
♂
H : brown
I : blue
= ♀
H : brown
I : blue
♂
H : lt. br.
I : blue
eyes crossed and weak in sun
= ♀
H : brown
I : blue
♂ V. H.
albino
♂
♀ E. H.
albino

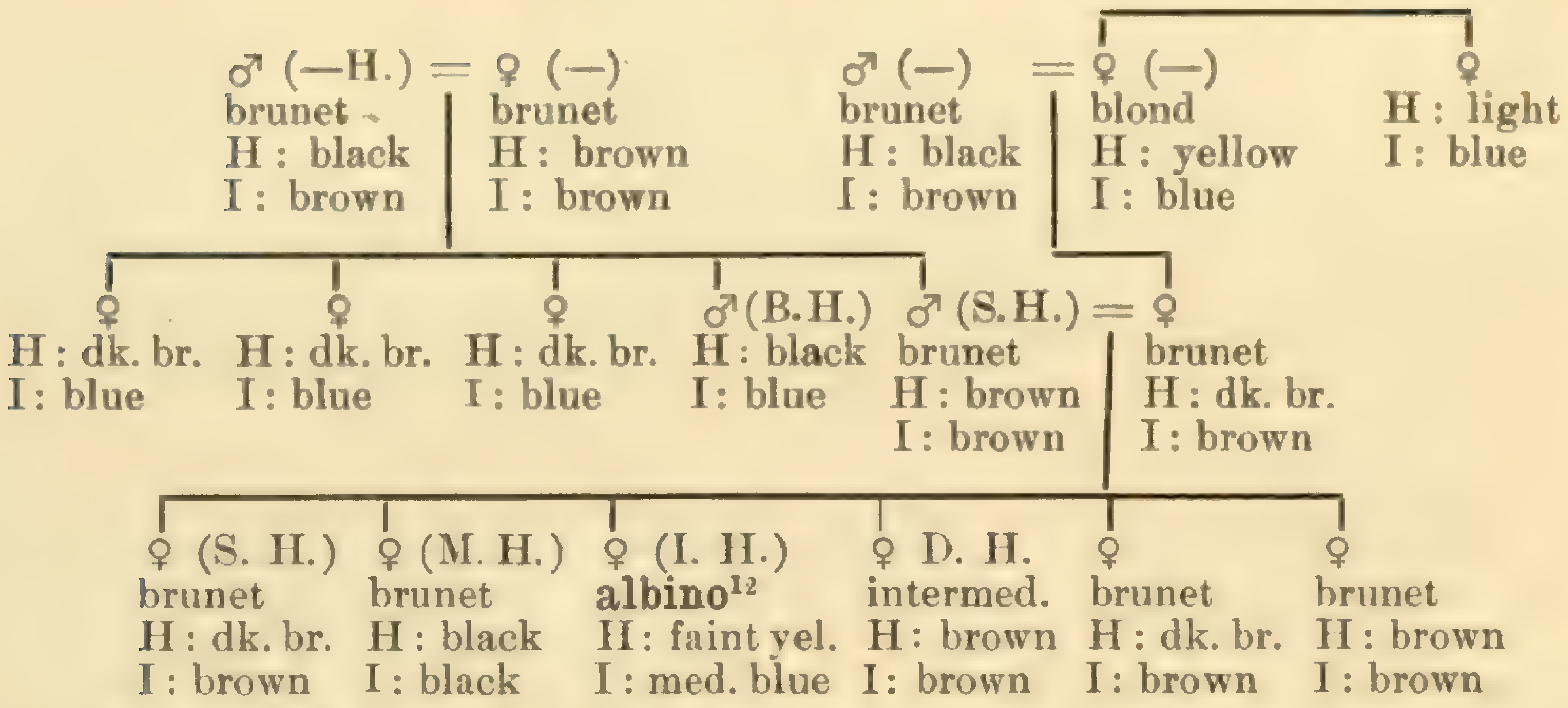
One son (which?) is cross-eyed.

12. Hor. Family


♂ (—H.)
H: med. br.
I: gray
= ♀ (L. K.)
H: dk. br.
I: dk. br.
♂ (E. M.)
H: light as child v. dk. br.
I: brown
= ♀
H: dk. br.
I: blue
♂ (J. E. H.)
H: dk. br.
I: gray
= ♀ (S. M.)
H: chestnut
I: brown
♀ (C. L. H.)
H: silver-white as child; lt. br.
I: blue
♀ (V. H.)
H: yellow as child; dk. br.
I: brown
♀ (E. H.)
H: yellow
I: blue
♂ (A. H.)
H: yellow as child
I: blue
♂ (G. H.)
H: yellow as child; lt. br.
I: blue
♀ (D. H.)
albino
H: originally white; at 10 years getting yellower
I: very lt. bl.; pupil pink

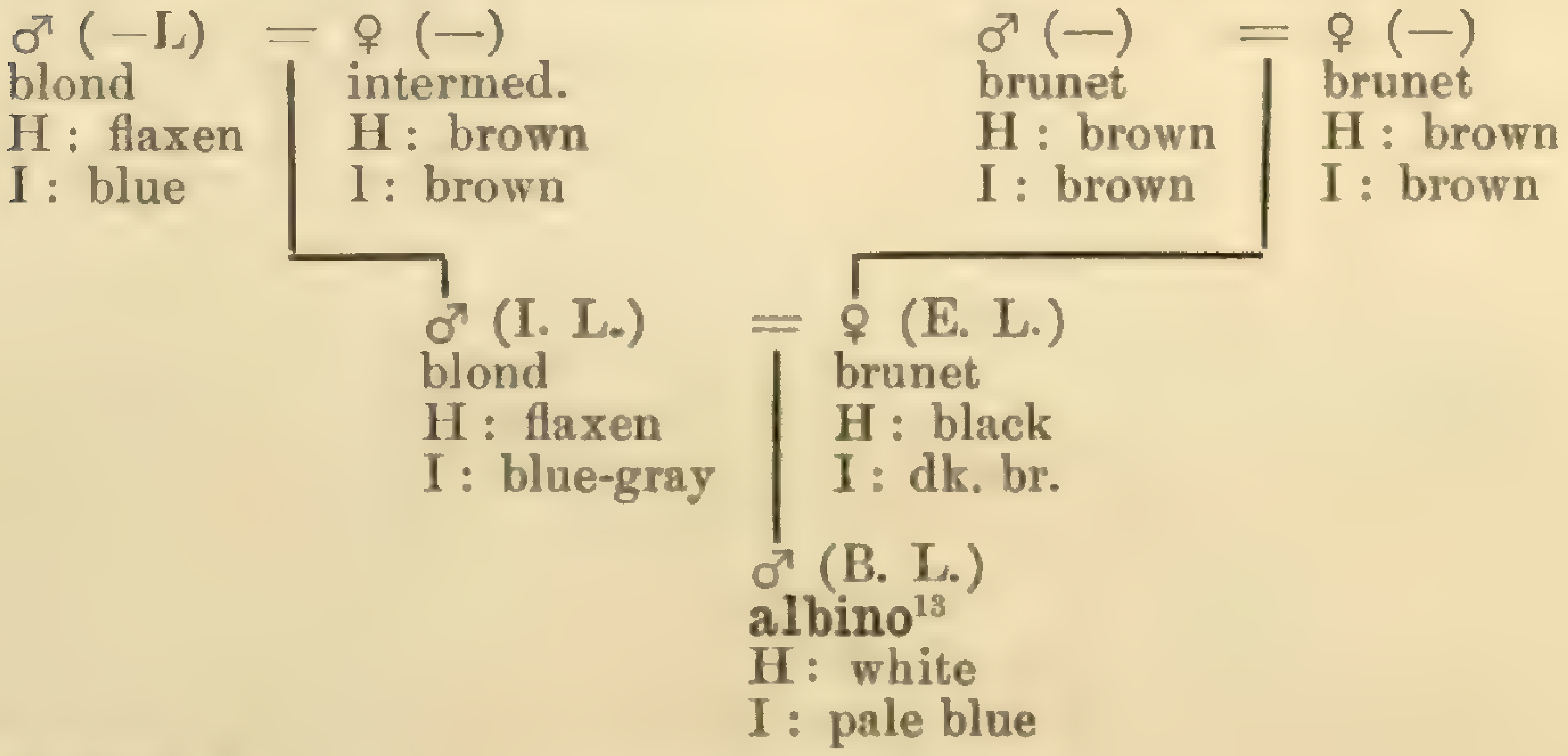
Seen by C. B. D. Nystagmus present.

13. Huf. Family (German Origin)


♂ (—H.) = ♀ (—)
brunet
H : black
I : brown
brunet
H : brown
I : brown
♂ (—) = ♀ (—)
brunet
H : black
I : brown
blond
H : yellow
I : blue
♀
H : light
I : blue
♀
H : dk. br.
I : blue
♀
H : dk. br.
I : blue
♀
H : dk. br.
I : blue
♂ (B.H.)
H : black
I : blue
♂ (S.H.) = ♀
brunet
H : brown
I : brown
brunet
H : dk. br.
I : brown
♀ (S. H.)
brunet
H : dk. br.
I : brown
♀ (M. H.)
brunet
H : black
I : black
♀ (I. H.)
albino[12]
H : faint yel.
I : med. blue
♀ D. H.
intermed.
H : brown
I : brown
♀
brunet
H : dk. br.
I : brown
♀
brunet
H : brown
I : brown

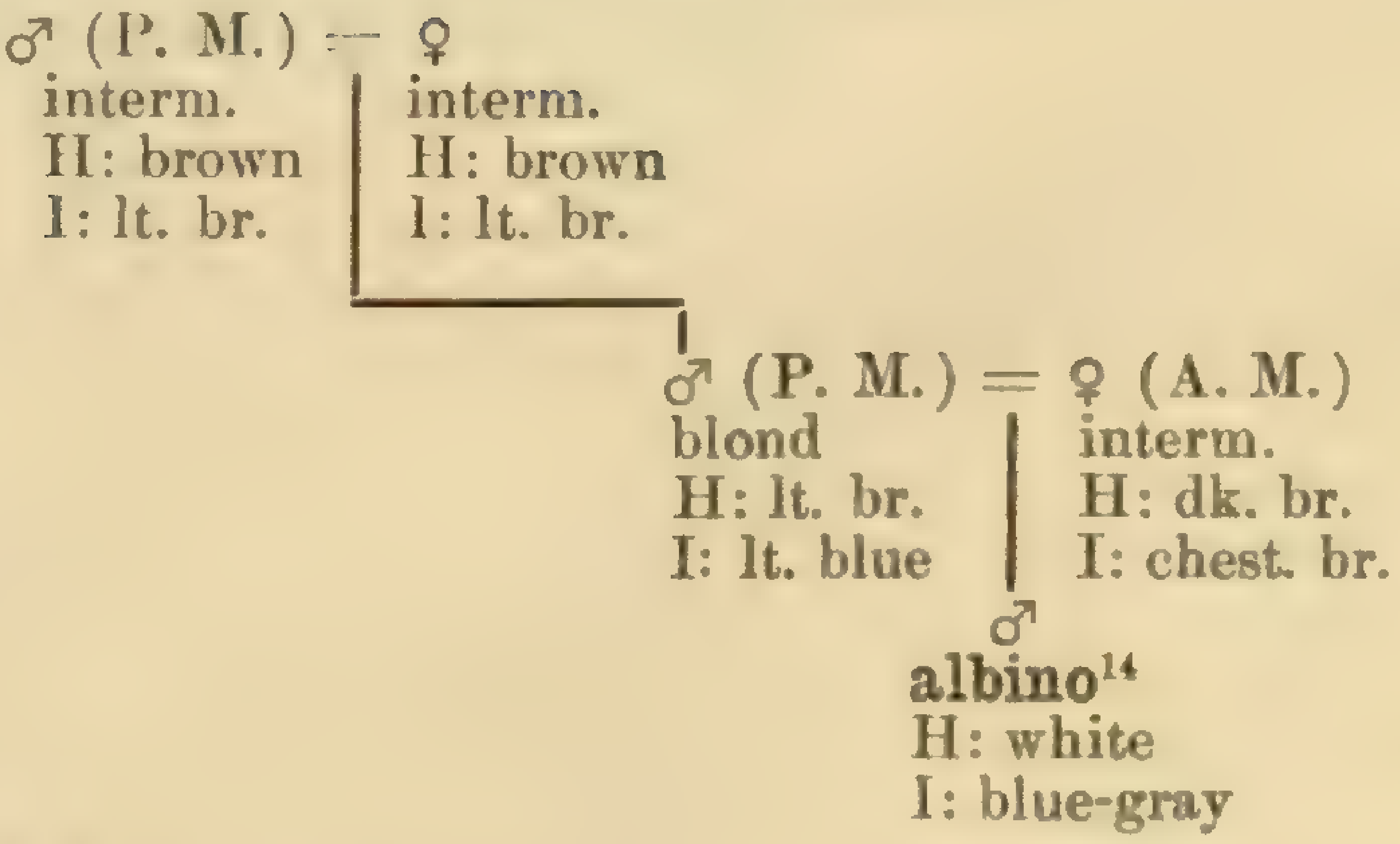
Seen by S. E.

14. Lie. Family


♂ (—L) = ♀ (—)
blond
H : flaxen
I : blue
intermed.
H : brown
I : brown
♂ (—) = ♀ (—)
brunet
H : brown
I : brown
brunet
H : brown
I : brown
♂ (I. L.) = ♀ (E. L.)
blond
H : flaxen
I : blue-gray
brunet
H : black
I : dk. br.
♂ (B. L.)
albino[13]
H : white
I : pale blue

Seen by S. E.

15. Mcg. Family


♂ (P. M.) = ♀
interm.
H: brown
I: lt. br.
interm.
H: brown
I: lt. br.
♂ (P. M.) = ♀ (A. M.)
blond
H: lt. br.
I: lt. blue
interm.
H: dk. br.
I: chest. br.
♂
albino[14]
H: white
I: blue-gray

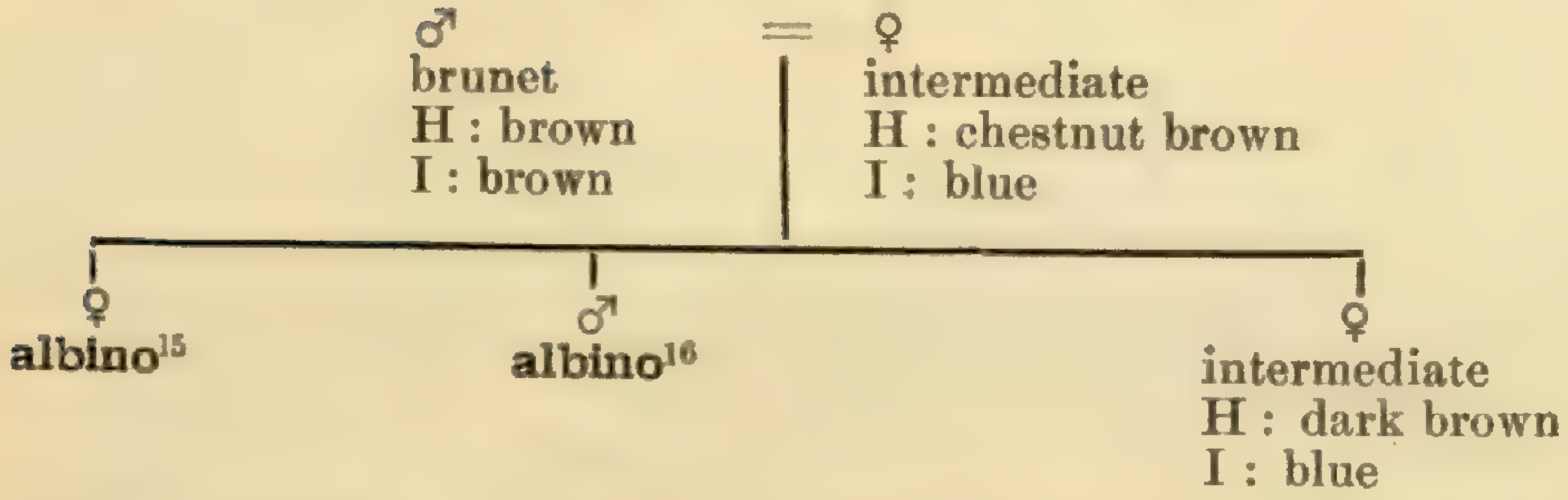
Seen by S. E.

[12] Retina with slight pinkish glow; nystagmus present in moderate degree; congenital hypermetropia.

[13] Retina pigmented; nystagmus present; nearsighted.

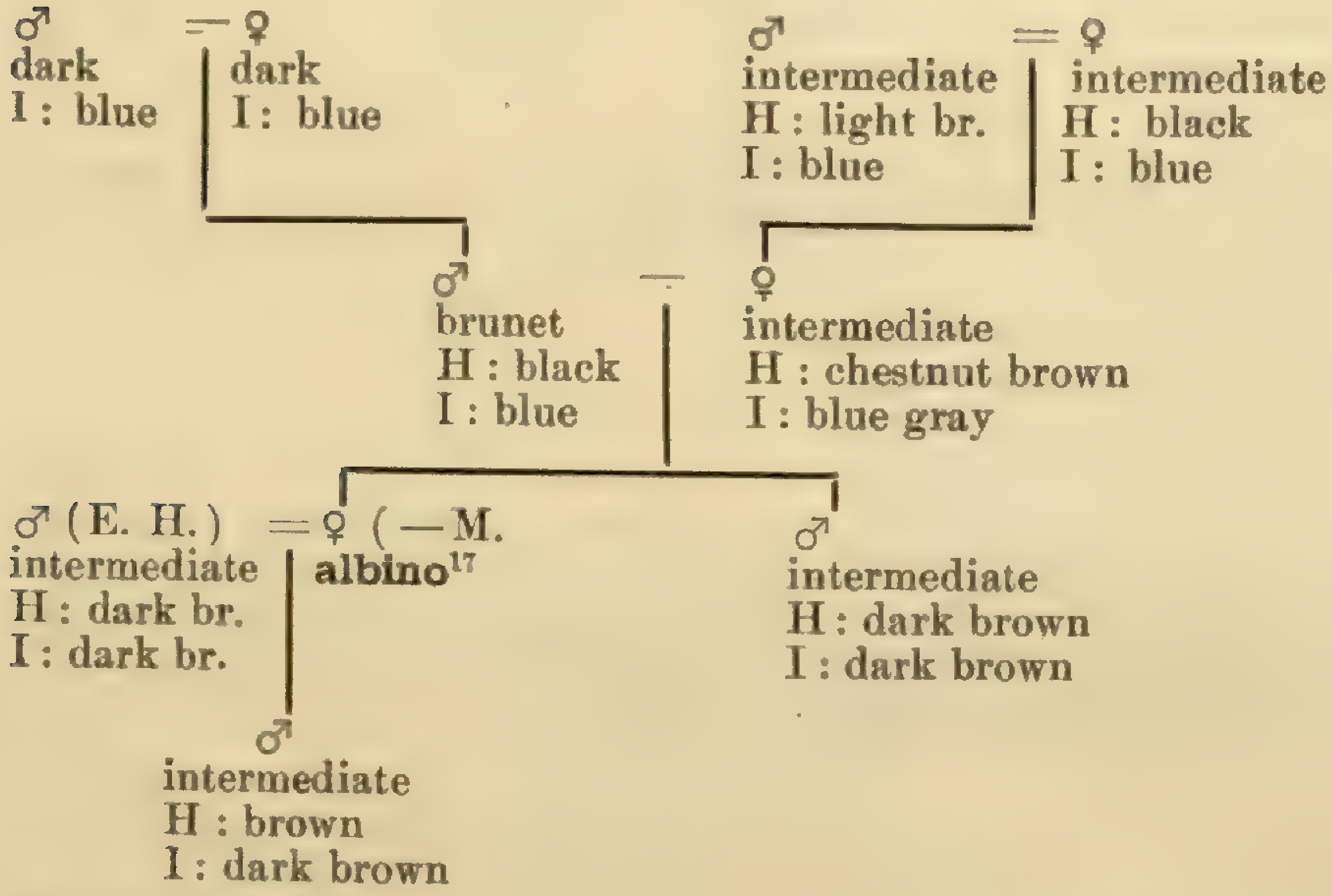
[14] Retina pinkish; nystagmus present; very slight internal strabismus; general intelligence; average at school work, reads readily; sight good except in bright light.

16. Mck. Family


♂
brunet
H : brown
I : brown
=
♀
intermediate
H : chestnut brown
I : blue
♀
albino[15]
♂
albino[16]
♀
intermediate
H : dark brown
I : blue

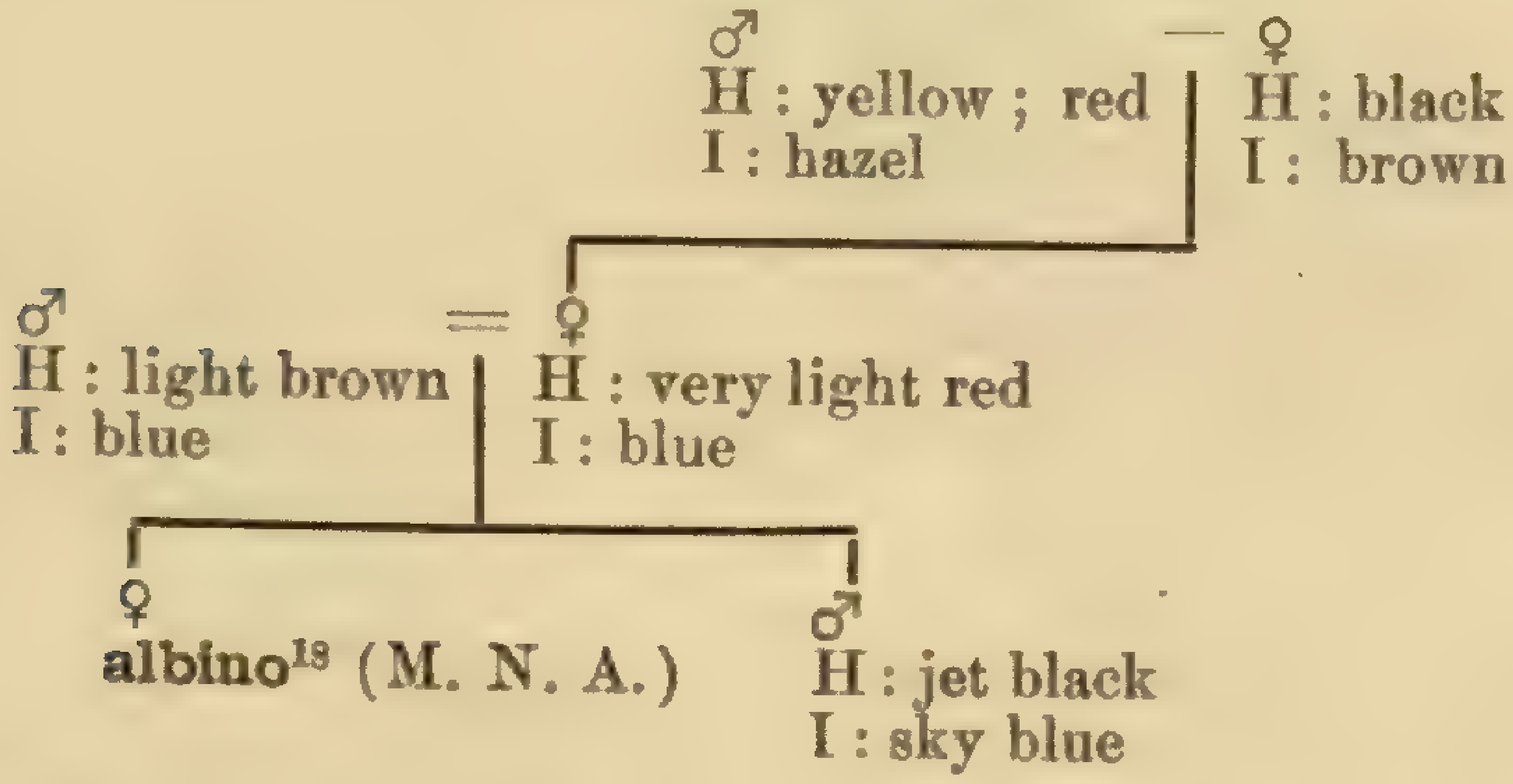
Seen by S. E.

17. Moo. Family


♂
dark
I : blue
=
♀
dark
I : blue
♂
intermediate
H : light br.
I : blue
=
♀
intermediate
H : black
I : blue
♂
brunet
H : black
I : blue
=
♀
intermediate
H : chestnut brown
I : blue gray
♂ (E. H.)
intermediate
H : dark br.
I : dark br.
=
♀ (—M.
albino[17]
♂
intermediate
H : dark brown
I : dark brown
♂
intermediate
H : brown
I : dark brown

Seen by S. E.

18. Nea. Family


♂
H : yellow ; red
I : hazel
—
♀
H : black
I : brown
♂
H : light brown
I : blue
=
♀
H : very light red
I : blue
♀
albino[18] (M. N. A.)
♂
H : jet black
I : sky blue

---

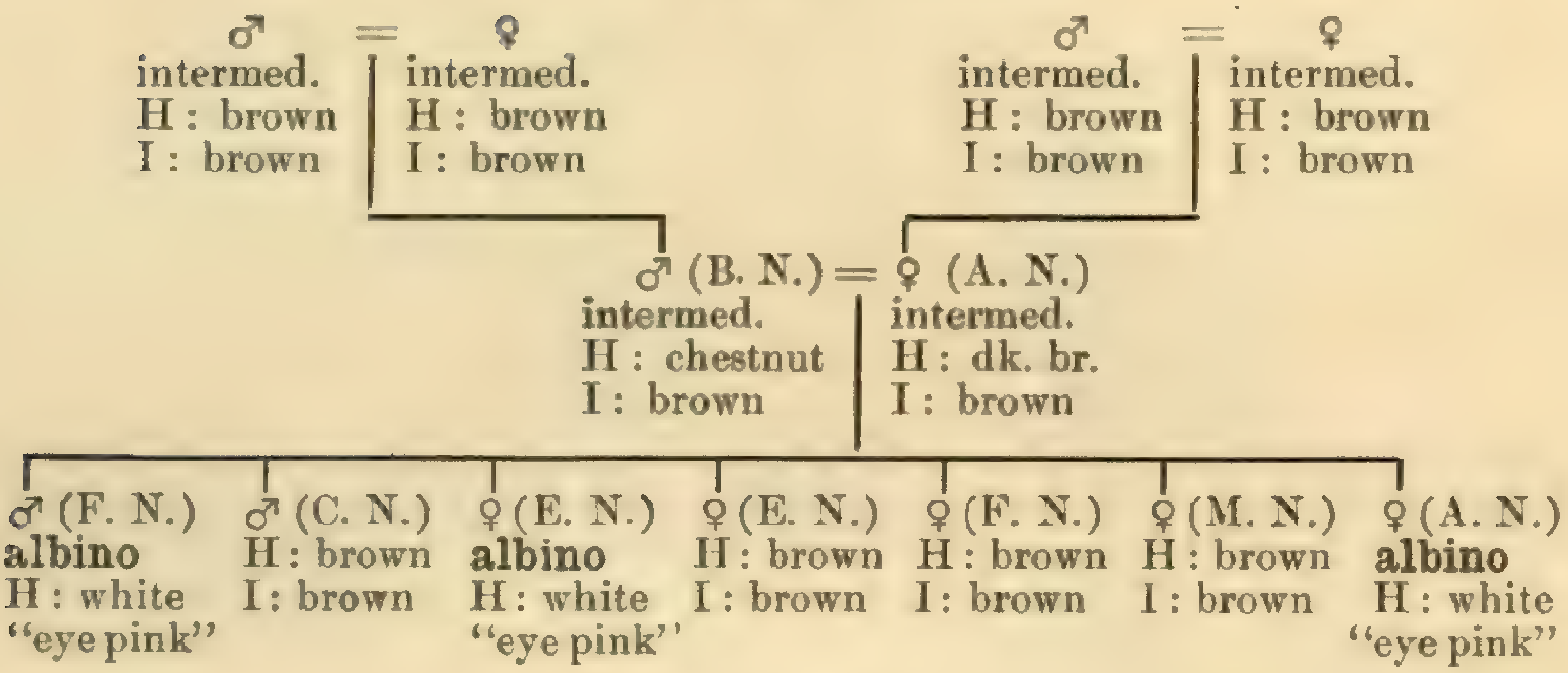
[15] Hair white; iris pale blue; retina pinkish as seen through pupil; nystagmus present; slight internal strabismus; work at school very difficult, sight growing weaker.

[16] Details as above. Eyes stronger, can read No. 9 point at 18 inches.

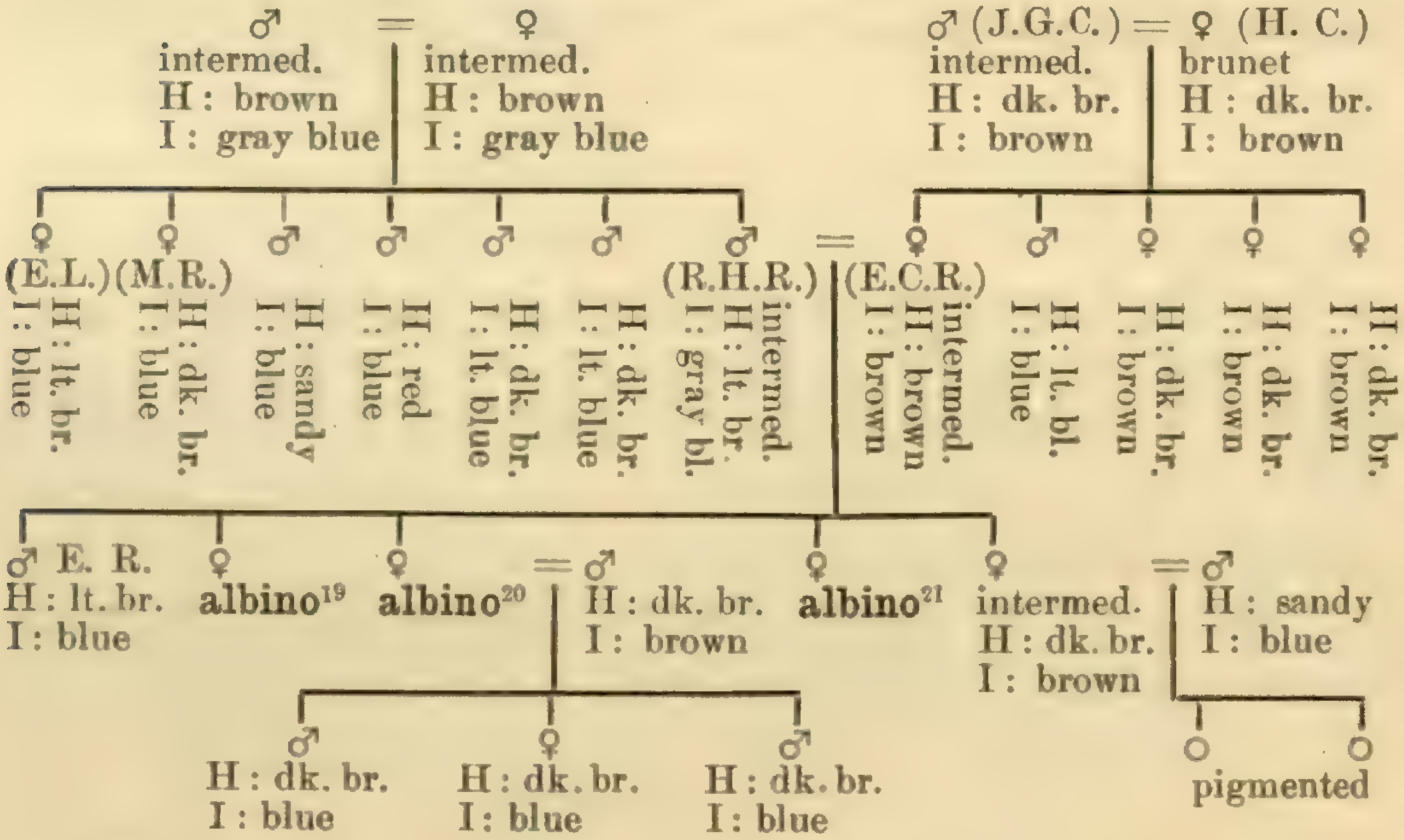
[17] Hair white; iris light blue, retina dark (almost black), nystagmus present, has congenital high degree of myopia. Fairly good at school, can see to sew at night, bright in conversation.

[18] Complexion very fair, hair white, iris clear blue.

19. NOG. FAMILY (ITALIAN)

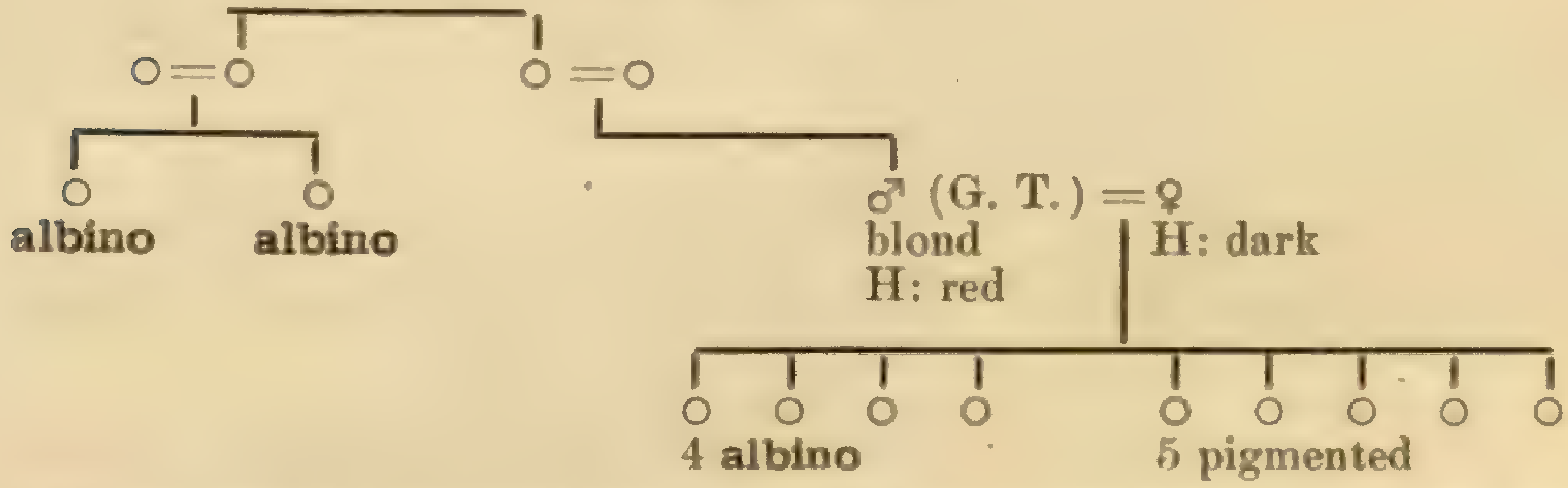

♂ = ♀
intermed.
H : brown
I : brown
intermed.
H : brown
I : brown
♂ = ♀
intermed.
H : brown
I : brown
intermed.
H : brown
I : brown
♂ (B. N.) = ♀ (A. N.)
intermed.
H : chestnut
I : brown
intermed.
H : dk. br.
I : brown
♂ (F. N.)
albino
H : white
"eye pink"
♂ (C. N.)
H : brown
I : brown
♀ (E. N.)
albino
H : white
"eye pink"
♀ (E. N.)
H : brown
I : brown
♀ (F. N.)
H : brown
I : brown
♀ (M. N.)
H : brown
I : brown
♀ (A. N.)
albino
H : white
"eye pink"

20. RID. FAMILY


♂ = ♀
intermed.
H : brown
I : gray blue
intermed.
H : brown
I : gray blue
♂ (J.G.C.) = ♀ (H. C.)
intermed.
H : dk. br.
I : brown
brunet
H : dk. br.
I : brown
♀ (E.L.) H : lt. br. I : blue
♀ (M.R.) H : dk. br. I : blue
♂ H : sandy I : blue
♂ H : red I : blue
♂ H : dk. br. I : lt. blue
♂ H : dk. br. I : lt. blue
♂ (R.H.R.) intermed. H : lt. br. I : gray bl.
=
♀ (E.C.R.) intermed. H : brown I : brown
♂ H : lt. bl. I : blue
♀ H : dk. br. I : brown
♀ H : dk. br. I : brown
♀ H : dk. br. I : brown
♂ E. R.
H : lt. br.
I : blue
♀ albino[19]
♀ albino[20] = ♂
H : dk. br.
I : brown
♀ albino[21]
♀ intermed.
H : dk. br.
I : brown
= ♂
H : sandy
I : blue
♂ H : dk. br. I : blue
♀ H : dk. br. I : blue
♂ H : dk. br. I : blue
pigmented

Seen by S. E.

21. THO. FAMILY


albino
albino
♂ (G. T.) = ♀
blond
H: red
H: dark
4 albino
5 pigmented

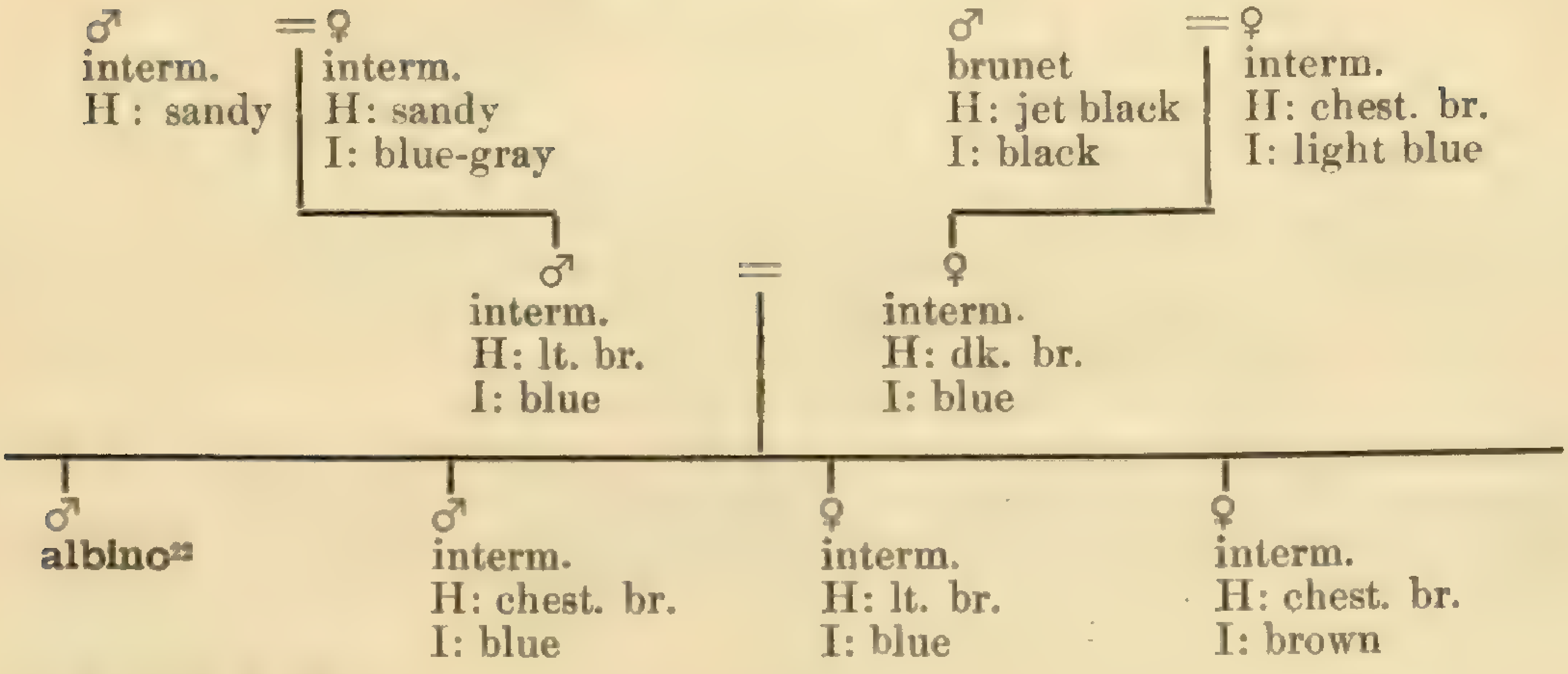
---

[19] Hair, faintly yellowish; iris, devoid of blue; retina with medium pinkish glow; nystagmus moderate; myopia, school work satisfactory; read a good deal; sparetime spent in weaving seats of cane chairs.

[20] Hair faintly yellowish; iris devoid of blue; retina with medium pinkish glow; nystagmus moderate; myopia; school work middling.

[21] Hair faintly yellowish; iris pale blue; retina with medium pinkish glow; nystagmus moderate; myopia; school work middling.

22. WIL. FAMILY

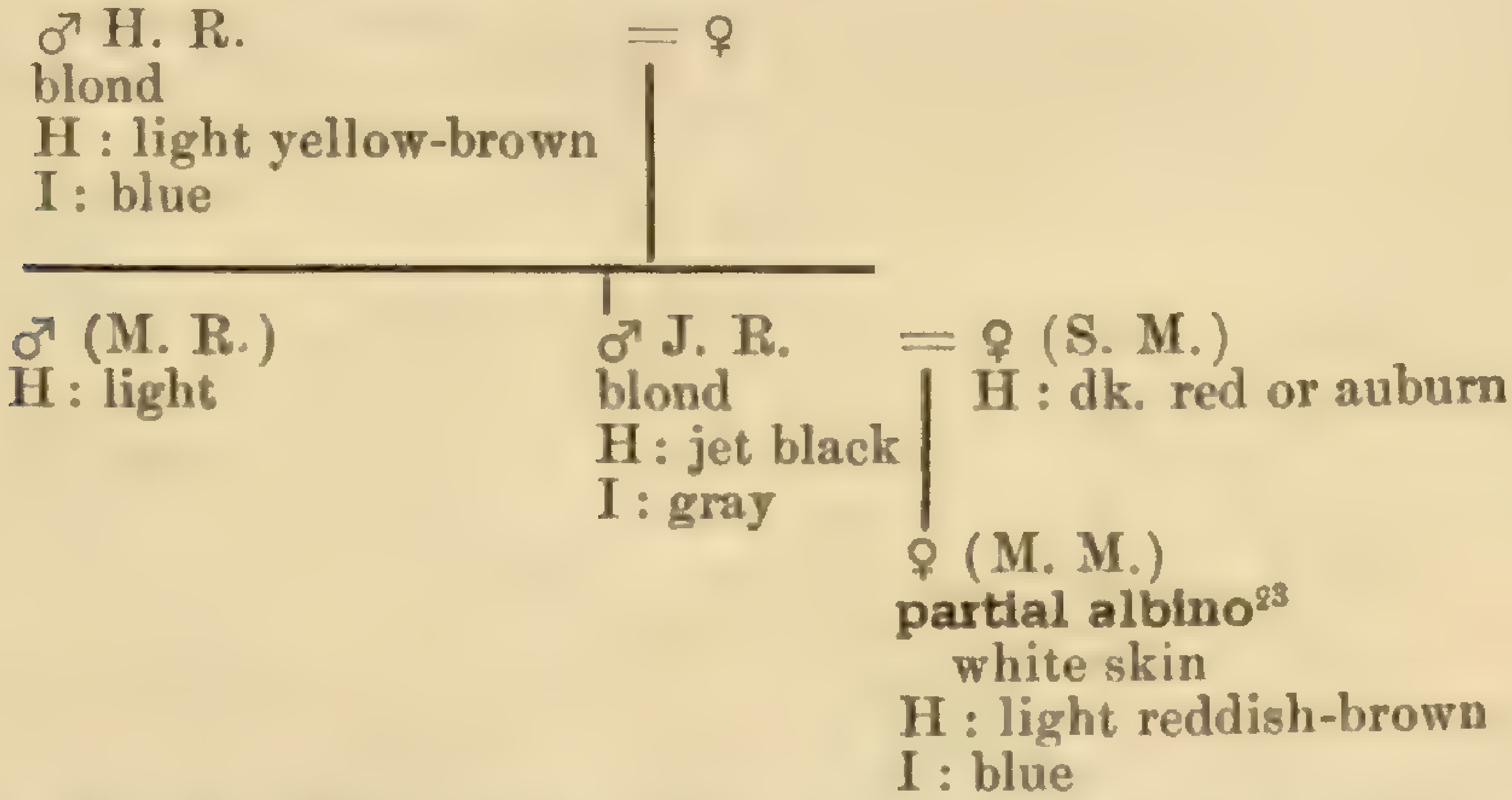

♂ interm. H: sandy
= ♀ interm. H: sandy I: blue-gray
♂ brunet H: jet black I: black
= ♀ interm. H: chest. br. I: light blue
♂ interm. H: lt. br. I: blue
= ♀ interm. H: dk. br. I: blue
♂ albino[22]
♂ interm. H: chest. br. I: blue
♀ interm. H: lt. br. I: blue
♀ interm. H: chest. br. I: brown

Seen by S. E.

23. The P-W family. The relationships of the members of this family, so far as worked out, are shown in the diagrams 23*a*, 23*b*, 23*c* and 23*d*. The persons in these diagrams come from the same general region and several surnames are common, especially those indicated by the initials P and W. The frequent recurrence of the same four surnames in the paternal and maternal sides of the ancestry of most of these albinos is testimony to a wide spread consanguinity. Further details are reserved for a later paper when it is hoped the pedigrees can be extended and connected.

(*d*) *Colored Families*

24. MER. FAMILY

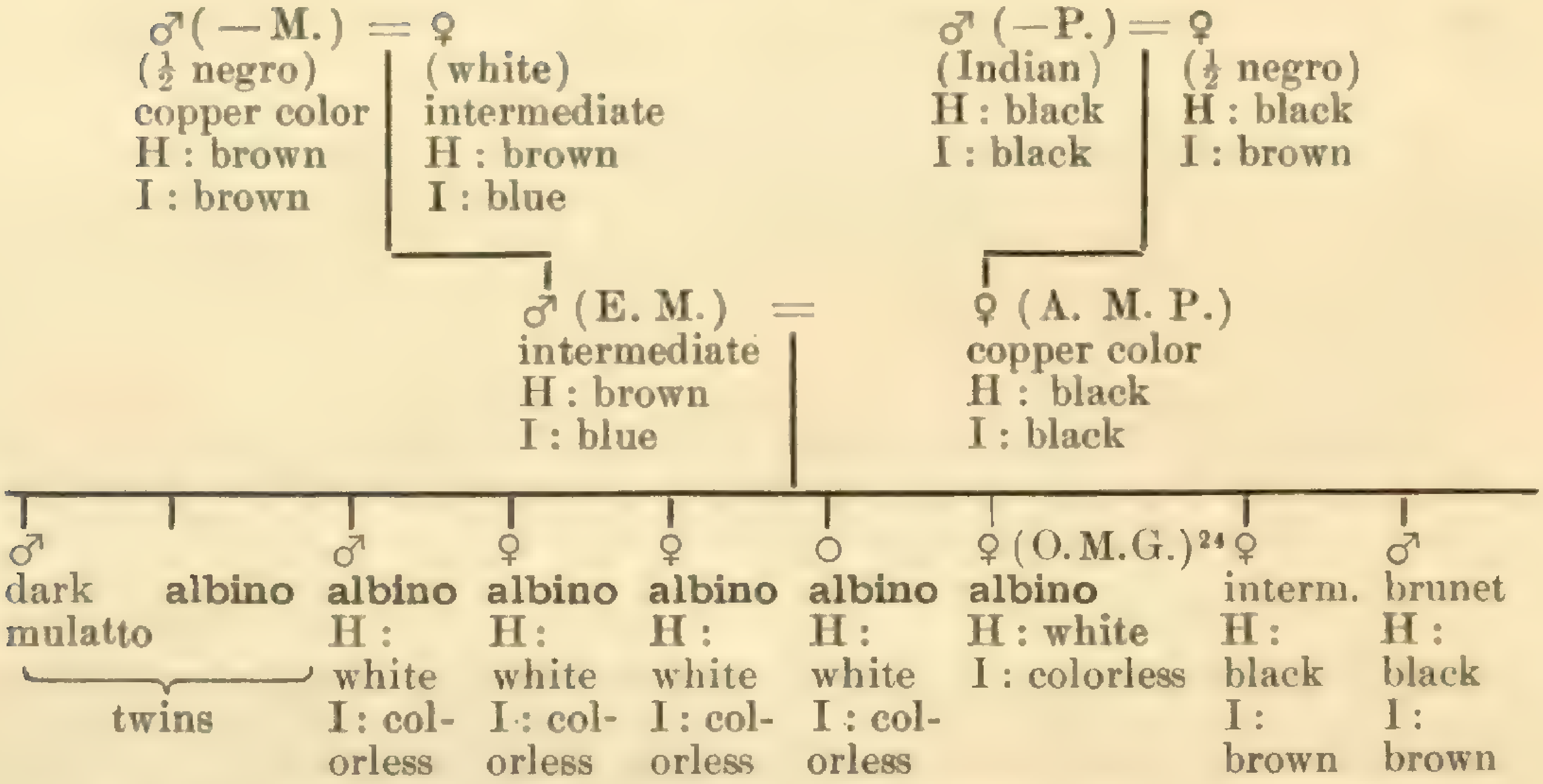

♂ H. R. blond H: light yellow-brown I: blue
= ♀
♂ (M. R.) H: light
♂ J. R. blond H: jet black I: gray
= ♀ (S. M.) H: dk. red or auburn
♀ (M. M.) partial albino[23] white skin H: light reddish-brown I: blue

---

[22] Hair white; iris pale blue; retina bright pink; nystagmus marked; eyes sensitive to bright light, sees better in half light. "Kept up with the rest in school."

[23] Seen by C. B. D. Retina not pink. Slight nystagmus.

25. MAN. FAMILY


♂ (—M.) = ♀
(½ negro)
copper color
H : brown
I : brown
(white)
intermediate
H : brown
I : blue
♂ (—P.) = ♀
(Indian)
H : black
I : black
(½ negro)
H : black
I : brown
♂ (E. M.) =
intermediate
H : brown
I : blue
♀ (A. M. P.)
copper color
H : black
I : black
♂ dark mulatto
albino
twins
♂ albino H : white I : colorless
♀ albino H : white I : colorless
♀ albino H : white I : colorless
○ albino H : white I : colorless
♀ (O.M.G.)[24] albino H : white I : colorless
♀ interm. H : black I : brown
♂ brunet H : black I : brown

Seen by S. E.

25. Under this head may be cited the observations of Dr. Hrdlicka, who has collected data concerning ten albino Hopi Indians and two albino Zuni.

It appears from his data that "albinos marry full-colored individuals of the opposite sex. They seldom raise any children and never have large families of their own." All of the albinos whose data follow have a pinkish-white skin and gray-blue or blue eyes. The color of hair varies from flaxen to light brown.

A summary of the data relating to inheritance of albinism is given in Tables A and B.

TABLE A

GIVING THE COLOR CONDITION OF THE FRATERNITY OF EACH ALBINO DESCRIBED. THE PARENTS ARE, IN ALL CASES, OF NORMAL COLOR.

No.	Sex.	Number of Fraternity.		No.	Sex.	Number of Fraternity.	
		Normal.	Albinic.			Normal.	Albinic.
1	♀	2+?	1	7	♀	4 or 5	1
2	♀	1+!	1	8	♀	2	1
3	♀	2	1	9	♀	1	1
4	♂	3	1	10	♂	3	1
5	♂	4	1	11	♂	7	1
6	♀	4	2	12	♂	4	2
				Total		37+ or 38+	14

---

[24] Retina pinkish; nystagmus present; myopic; can read nine point print at five inches.

TABLE B

Giving the Number of Normal and of Albinic Offspring of an Albinic Individual Married to a Normal.

N, normal; A, albinic, D, the dominant character; R, the recessive.

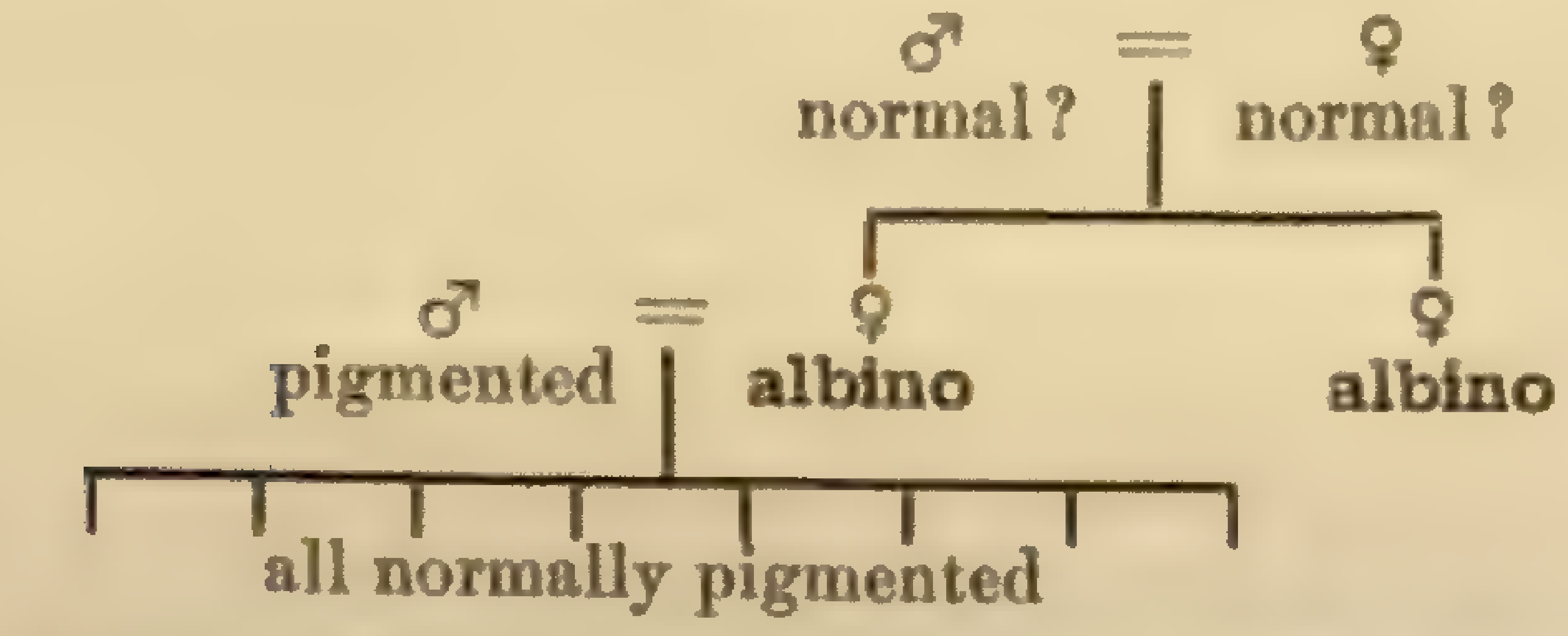
D	R	DR (=N)	RR (=A)
N♀	A 4♂[25]	0	0
N♂	A 7♀	0	0
N♂	A 9♀	1	0
N♀	A11♂	1	0
		2	0

If we consider *both* parents of the fourteen albinos listed in Table A as simplex in pigment, *i. e.*, as having not only normal but also albinic germ-cells, they were "DR's." When two such simplex (DR) individuals are mated, we expect 25 per cent. of the offspring to be duplex (DD), 50 per cent. simplex (DR or RD), and 25 per cent. without pigment (RR). Only the last will be albinic, 75 per cent. will be of normal color. We actually find that with fourteen albinos there are associated in their fraternities 37 + or 38 + normal individuals, expectation being 42. The deficiency would doubtless be accounted for by the unincluded normal children. Since the proportion of albinic offspring in the given fraternities accords with expectation on the assumption that albinism is recessive that assumption is justified.

Second, if albinism is recessive, it should not appear in offspring of albinos with normal consorts. Unfortunately the sterility of the cross makes it difficult to get the desired data, but so far as they go, they are not in disaccord with hypothesis.

III. One Parent Albinic

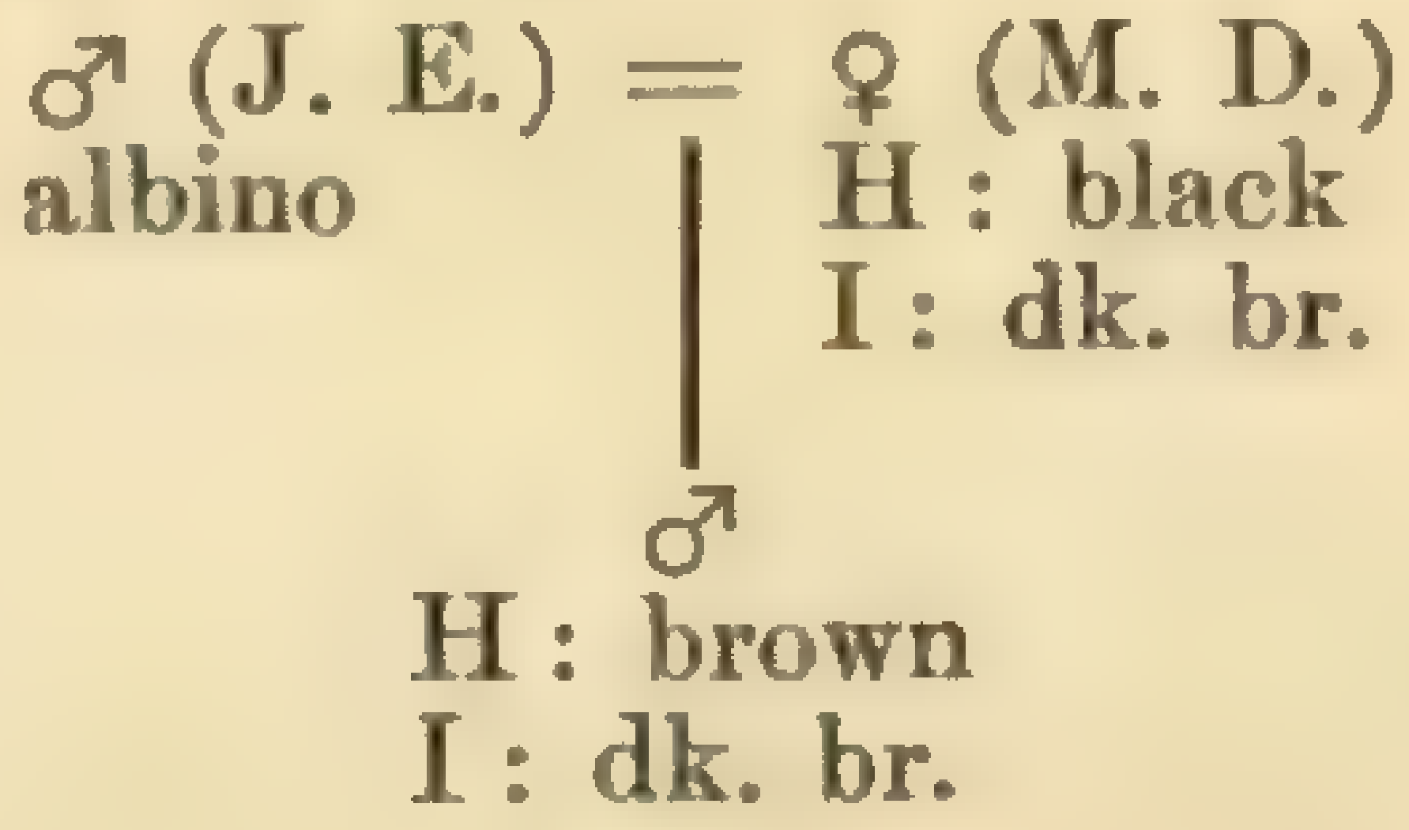
26. Edd. Family



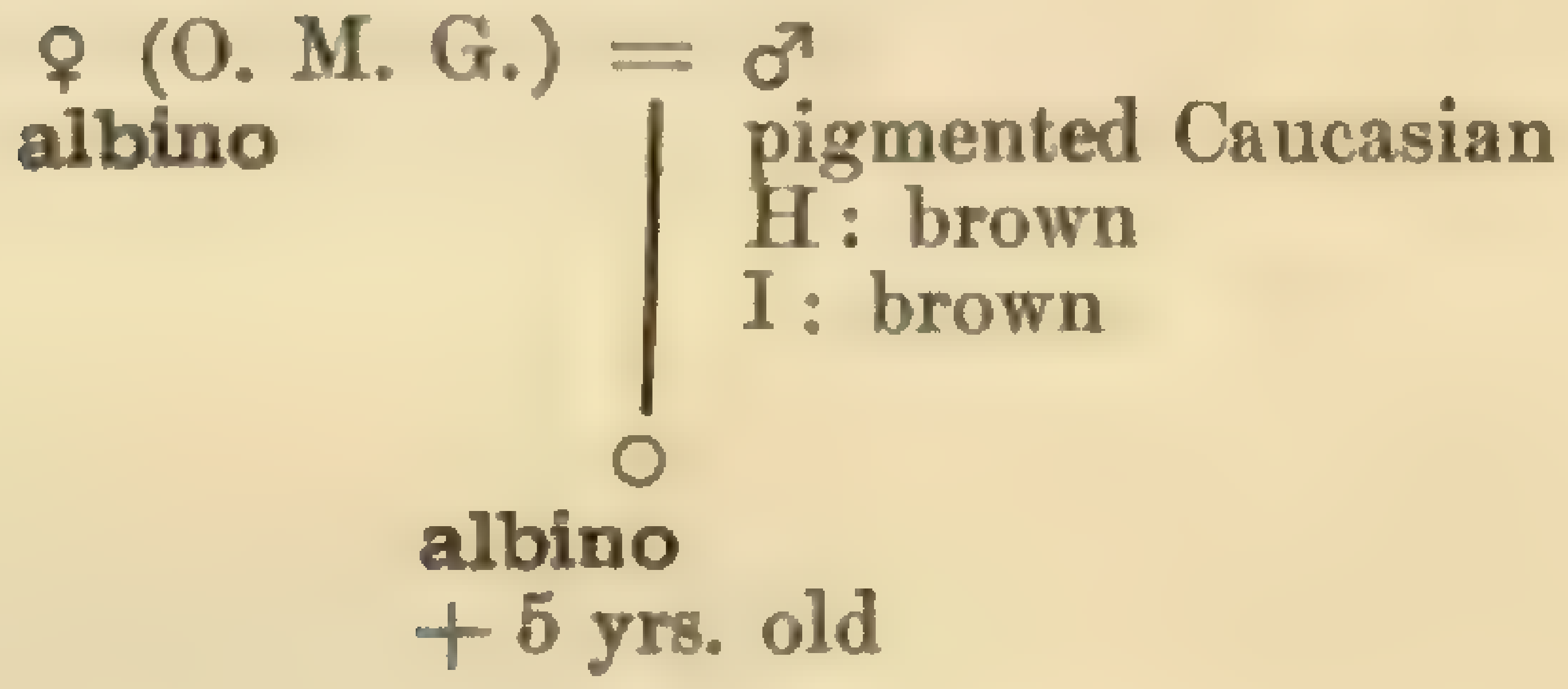
---

[25] These numbers refer to the serial numbers of the cases as given in Table A.

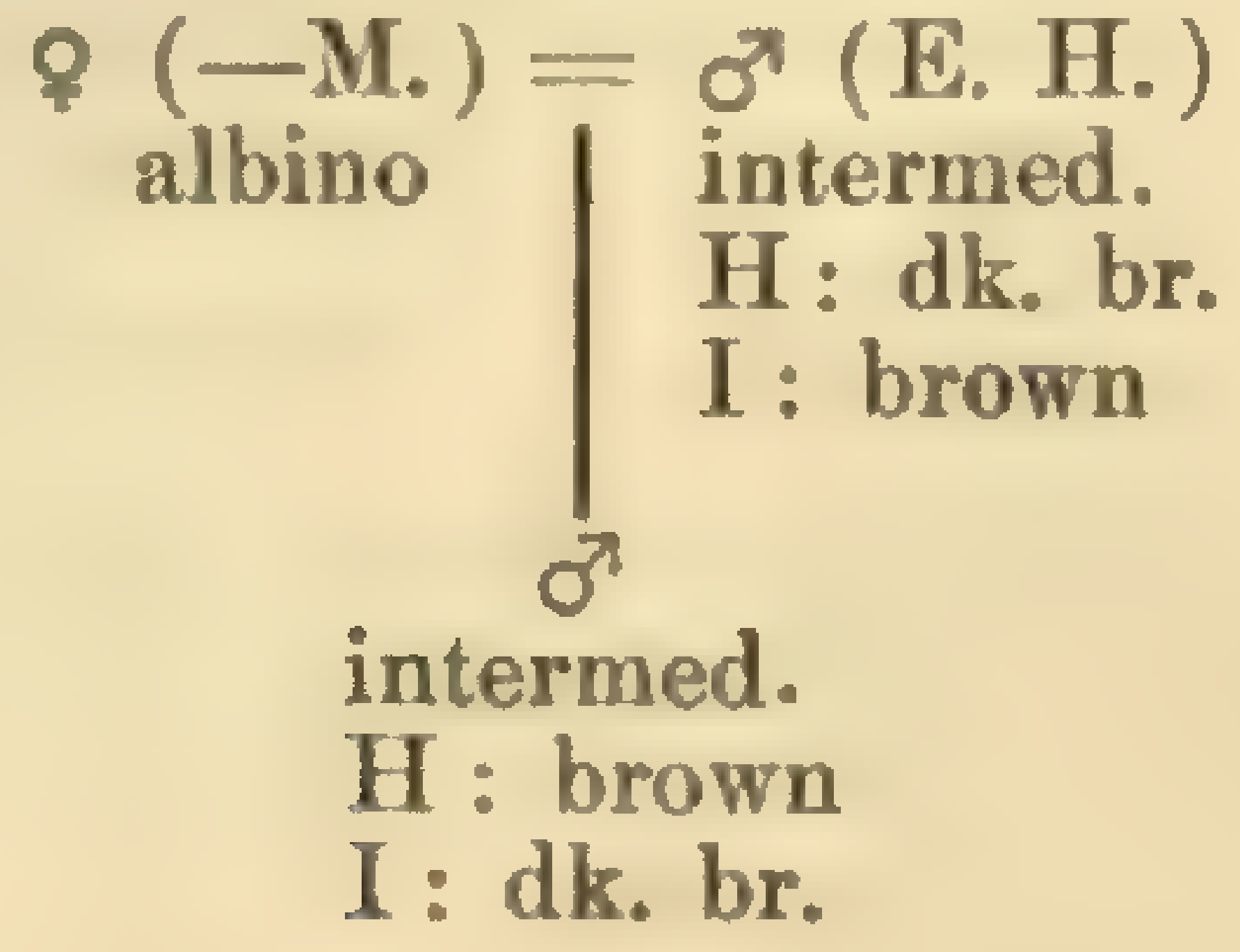
27. ENN. FAMILY (CONTINUATION OF NO. 5)


♂ (J. E.) = ♀ (M. D.)
albino
H : black
I : dk. br.
♂
H : brown
I : dk. br.

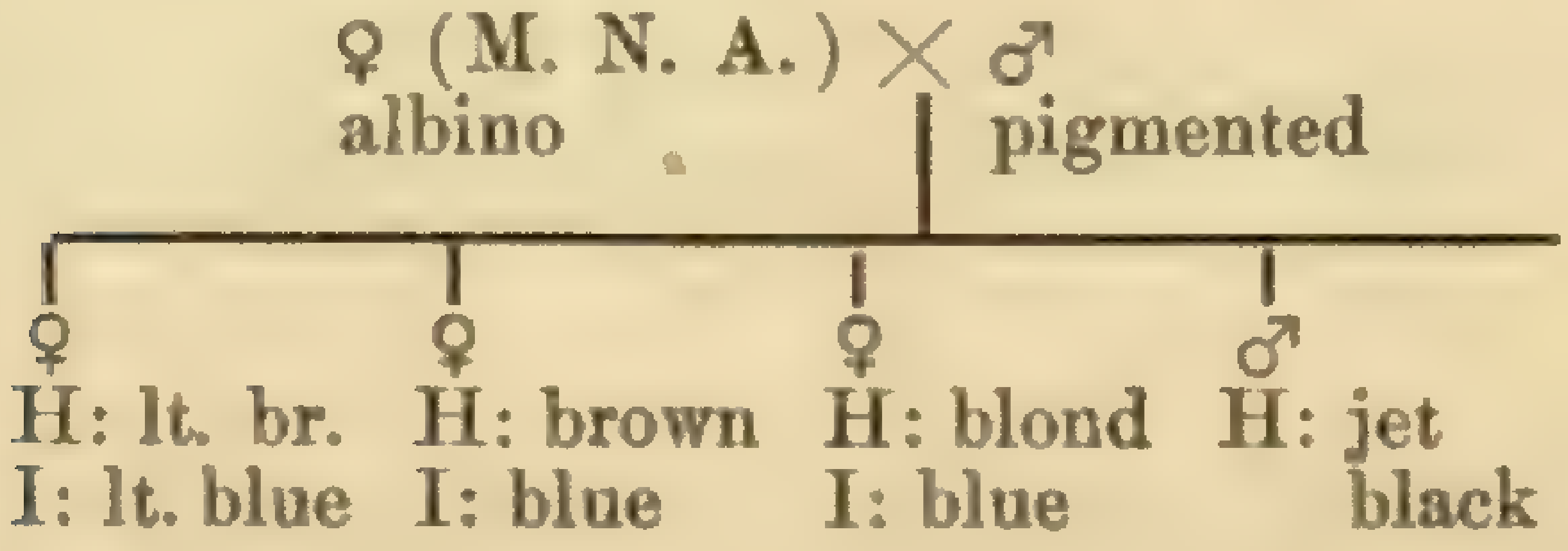
28. MAN. FAMILY (CONTINUATION OF NO. 24)


♀ (O. M. G.) = ♂
albino
pigmented Caucasian
H : brown
I : brown
○
albino
+ 5 yrs. old

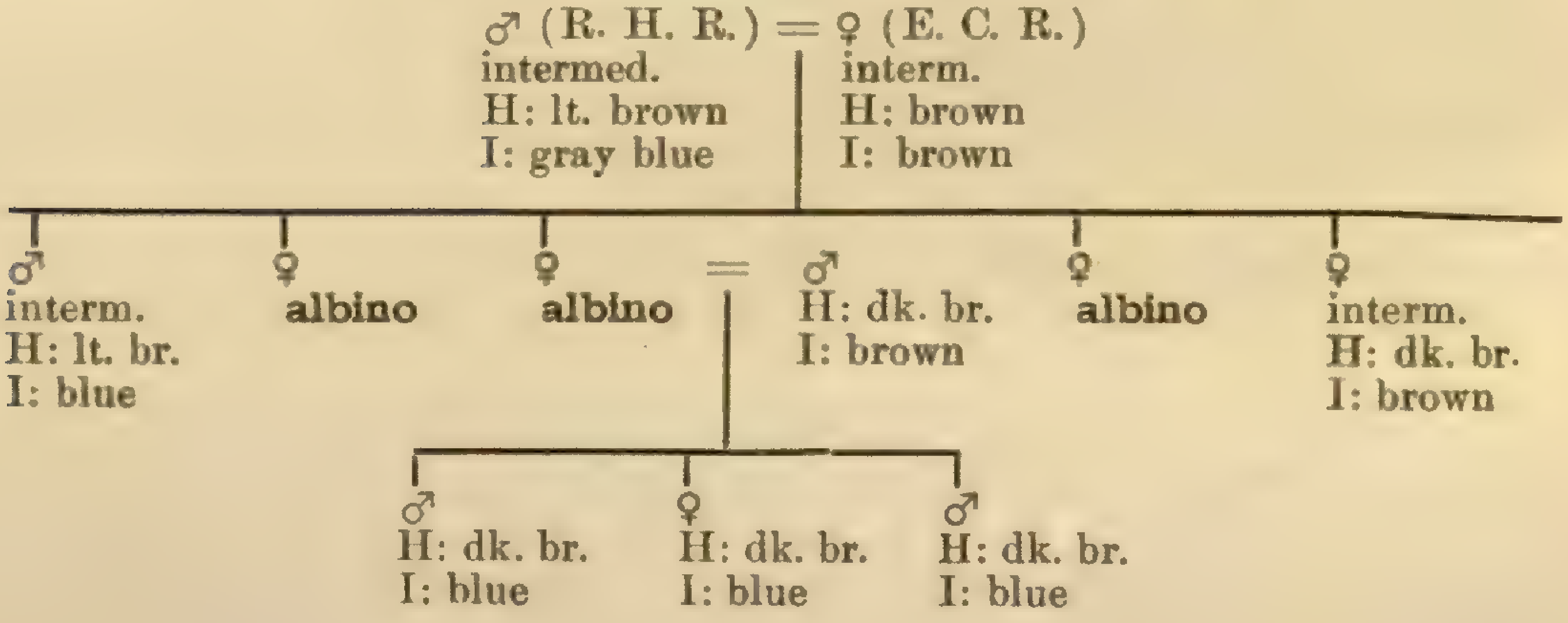
29. MOO. FAMILY (CONTINUATION OF NO. 17)


♀ (—M.) = ♂ (E. H.)
albino
intermed.
H : dk. br.
I : brown
♂
intermed.
H : brown
I : dk. br.

30. NEA. FAMILY (CONTINUATION OF NO. 18)


♀ (M. N. A.) × ♂
albino
pigmented
♀
H: lt. br.
I: lt. blue
♀
H: brown
I: blue
♀
H: blond
I: blue
♂
H: jet black

31. RID. FAMILY (CONTINUATION OF NO. 20)


♂ (R. H. R.) = ♀ (E. C. R.)
intermed.
H: lt. brown
I: gray blue
interm.
H: brown
I: brown
♂
interm.
H: lt. br.
I: blue
♀
albino
♀
albino
=
♂
H: dk. br.
I: brown
♀
albino
♀
interm.
H: dk. br.
I: brown
♂
H: dk. br.
I: blue
♀
H: dk. br.
I: blue
♂
H: dk. br.
I: blue

IV. The D. G. V. Family (see Plate)

This remarkable family comprises a great mixture of white, negro and even Indian blood, as well as many consanguineous marriages. The Man family comes from the same rural community, but its connections with the D. G. V. family have not yet been established. It will be observed that every albino has the blood of all three families D., G. and V., so it can not be said, at present, from which family albinism originally came. It will be noted, also, that both of the youngest family (whose history is best known) arise from cousin marriages. Considering only those families in which albinism actually occurs there are 8 albinos in 22 children, which is a greater proportion than the expected 25 per cent. (5 or 6 albinic offspring). It is clear, however, that it may well be that there is potential albinism in one or more of the families with 3 to 5 children, in which by chance it fails to appear—the 22 children are merely a minimum.

Details about some of the persons in this family follow:

V.[1] 7, Yellowish complexion, brown hair and iris.

V. 8, Yellowish complexion, light brown hair, blue iris.

V. 9, An almost white mulatto, very light brown hair, blue iris.

V. 10, An almost white mulatto, brown hair, blue iris.

VI. 4, Intermediate complexion, light brown hair, gray iris.

VI. 5, Yellowish complexion, light brown hair, blue iris.

VII. 1, T. V., aged 3, albino, hair white, iris colorless, retina with pinkish glow, nystagmus present, intellectually bright and well developed.

VII. 2, F. V., aged 4, intermediate complexion, hair and iris dark brown.

VII. 3, M. V., aged 1, brunet, hair and iris black.

V. 20, J. V. (Indian, French and negro blood), yellow skin, very light brown hair, yellow iris.

[25a] The Roman numeral refers to the generation; the Arabic to the individual.

TABLE IX

Showing the Hair and Eye Color of Parents and Grandparents of Albinos arising from Pigmented Parents

No.	Name.	Father.		Mother.		F.F.		F.M.		M.F.		M.M.	
		Hair.	Eye.	Hair.	Eye.	Hair.	Eye.	Hair.	Eye.	Hair.	Eye.	Hair.	Eye
4.	She.	br	br	dk.br	br	br	br	yell.br	bl	N	br	lt.br	bl.
5.	Enn.	N+R	br	N(+R)	dk.br	lt.yell.br.	dk.bl	N	dk.br	yell.br	lt.br	N	dk.br
7.	Sac.	gold	bl	gold	bl	gold	lt.bl	br	dk.br	N	N	yell.br	bl.gr
7a.	Bro.-7	dk.br	N	dk.br	bl.	—	—	—	—	—	—	—	—
8.	Don	br+R	bl	lt.goldbr.	bl	dk.br	bl	br	bl	flax	bl	chest.br	bl
9.	Ed.	N	br	chest.br	bl	N	br	br	br	—	—	chest.br	gray bl
10.	Far.	chest	chest.br	br	br	chest.br	bl	br	br	dk.br	br	chest.br	bl
11.	Fer.	br	bl	N	dk.br	N	—	N	N	lt.br	lt.gray	N	dk.br
11a.	Hlo.	br	bl	br	bl	br	lt.br	br	br	br	bl	br	bl
12.	Hor.	dk.br	gray	chest	br	br	gray	dk.br	dk.br	lt. to dr.br	br	dk.br	bl
13.	Hut.	br	br	dk.br	br	N	br'	br	br	N	br	yell.	bl
14.	Lie.	flax	bl.gray	N	dk.br	flax	bl	br	br	br	br	br	br
15.	Meg.	lt.br	lt.bl	dk.br	chest.br	br	lt.br	br	lt.br	—	—	—	—
16.	Mck.	br	br	chest.br	bl	—	—	—	—	—	—	—	—
17.	Moo.	N	bl	chest.br	bl.gray	—	bl	—	bl	lt.br	bl	N	bl
18.	Nea.	lt.br	bl	v. lt. red	bl	—	—	—	—	yell.red	hazel	N	br
19.	Nog.	chest	br	dk.br	br	br	br	br	br	br	br	br	br
19a.	Pit.	N	N	dk.br	bl	light	blue	N	N	light	bl	N	br
20.	Rid.	lt.br	gray bl	br	br	br	gray bl	br	gray bl	dk.br	br	dk.br	br
21.	Tho.	red	—	dark	—	—	—	—	—	—	—	—	—
22.	Wil.	lt.br	bl	dk.br	bl	sandy	—	sandy	bl.gray	N	N	chest.br	lt.bl

V. 21, M. (Irish origin), brunet, black hair, blue iris.

VI. 10, J. V., Brunet, brown hair, blue iris.

VI. 11, S. G., Intermediate complexion, brown hair and iris.

VII. 15, A. V., Aged 18, albino, white hair, colorless iris, retina pinkish, nystagmus present, mentally quick.

VII. 18, L. V., Aged 24, albino, white hair, colorless iris.

V. THE CONDITION OF HAIR AND EYE COLOR IN THE PIGMENTED PARENTS OF ALBINOS

Assuming all pigmented parents of albinos to be simplex in pigment we may inquire if such simplex parents differ from the population at large in their hair and eye color. To get an answer to this inquiry Table IX has been drawn up.

This table is summarized in Table X, so as to bring out the relative frequency of the different types.

TABLE X

THE RELATIVE FREQUENCY OF THE DIFFERENT TYPES OF HAIR AND EYE COLOR IN THE PARENTAGE OF ALBINOS

Hair Color.								Eye Color.							
Types.	F.	M.	FF.	FM.	MF.	MM.	Total.	Types.	F.	M.	FF.	FM.	MF.	MM.	Total.
N (black)	3	2	3	3	3	5	19	N (black)	2			2	2		6
dk. br.	2	8	1	1	2	2	16	dk. br.		3		3		2	8
br.	5	3	6	10	4	3	31	br.	6	6	4	5	7	5	32
lt. br.	4				2	1	7	lt. br.			2	1	1		4
golden	1	2	2	1	1	1	8	chest. br.	1	1					2
yellow						1	1	hazel					1		1
flaxen	1		1		1		3	gray	1		1		1		3
red+N	1	1					2	blue-gray	2	1	1	2		2	8
red+dk.br.	1						1	blue	7	9	6	4	4	7	37
chestnut	2	4	1			3	10	lt. blue	1		1			1	3
red	1	1			1		3								
Total	21	21	14	15	14	16	101	Total	20	20	15	17	16	17	105

If Table X be compared with the proportional distribution of the different types of hair color in the population at large, certain differences are seen. Thus while black, dark brown and brown hair constitute in a random population (Holmes and Loomis, 1909, p. 55) 695 out of 853 persons, or 81.5 per cent., in Table X, they constitute only 65 per cent. On the other hand, while, according to Holmes and Loomis (1909, Table III), red and auburn constitute only about 5.5 per cent. of their population, the various forms of red constitute 16 per cent. of the population of Table X, or three times the typical proportion. It appears then that, on the whole, the pigmented ancestry of albinos shows an excess of red and the weaker grades of melanic pigment.

The distribution of eye color, on the other hand, shows little that is abnormal. The "blacks" are somewhat deficient, about 70 per cent. as abundant as in the population as a whole, the browns are in excess, and the blues occur in nearly normal proportions. The last result was hardly anticipated as it might have been expected that the pale blue iris of the albino would be specially apt to proceed from blue-eyed parents, but this is not so. As a matter of fact, dark brown eyes are quite compatible with recessive albinism as Table XI shows. The general teaching of Table XI is that the heterozygous or simplex pigmentation of the offspring is not always clearly less than that of the darker parent. But, on the whole, blue iris predominates slightly and the hair tends to run

TABLE XI

Showing the Hair and Iris Color of the Offspring of an Albino and a Pigmented Parent

Family.	Parents.			Offspring.	
	Albino.	Pigmented Parent.		Hair Color.	Iris Color.
		Hair Color.	Iris Color.		
Enn.	♂	N	dk. br.	br	dk. br.
Moo.	♀	dk. br.	dk. br.	br.	dk. br.
Nea	♀	pigmented	pigmented	lt. br.	lt. br.
				br.	blue
				blond	blue
				jet black	—
Rid.	♀	dk. br.	br	dk. br.	blue
				dk. br.	blue
				dk. br.	blue

lighter than, or at least not to exceed, that of the darker parent.

VI. The Origin and "Cause" of Albinism

The question remains to be discussed: What is the origin and "cause" of these albinos. The general conclusion seems justified, as in other mammals so in man, albinism is due to the fortuitous union of two germ-cells lacking this factor so that it is absent in the zygote whence the albino proceeds.

The objections to this view are three: (1) The usual absence of any history of albinism in the family; (2) the improbability of so frequent unions of two persons bearing albinism recessive; (3) the lack of statistical accord of the results of human breeding with those of animals.

The first objection is not valid for any one who has done experimental breeding, because he knows full well how the recessive condition may be carried unexpressed in the germ-cells for many generations awaiting that chance conjugant that also carries the recessive condition. Absence of any history of albinism in a family has the less significance in a country like ours where a large proportion of the population can not tell the names of their grandparents and know little of their cousins, who may, indeed, live one to three thousand miles away.

The improbability of so frequent unions of two or three persons having albinism recessive has been referred to by Pearson. With a mathematical showing, he tells the story of an albino who married successively two pigmented (?) husbands and had some albino children by each. "All three stocks, according to Mendelian hypothesis, ought to have albinism in a recessive form. You can calculate the chances against that because an albino occurs in Italy about 1 in 30,000, in Norway, about 1 every 20,000 of the population, in Scotland, 1 in 24,000. What are the chances that a woman of albinotic stock should marry two stocks affected with albinism and not related either to her or to each other?" The inference seems to be that Pearson would be content with "calculating the chances" and, because the ratio was small, insisting that the three stocks could not all have albinism recessive. Such a method of procedure is, I fear, all too characteristic of the "careful work" which alone, according to its editor, is admitted to the pages of *Biometrika*.[26] Of course the facts are that we have here no data for calculating the required chances. In the first place, the term "not related" has only a relative significance in the statistics of human qualities; it usually means not first cousin or nearer relative, more rarely extends to second cousin, or at the outside, to third cousin. And yet two persons of the grade of tenth cousin may easily carry recessive an albinic condition derived from a common source. A fairer question would be, what are the chances that a woman shall marry in succession two men related between the grades of third and tenth cousin, supposing, further, all three come from the same rural district, long settled and relatively stable? I think the conditions that Pearson does not cite might easily render the chances several million to one in favor of the three persons being less distantly related than tenth cousin. An actual illustration of this condition of affairs is shown in the D. G. V. and P. W. families. The three family names represented by D., G. and V. occur again and again in this family, as the pedigree table shows. Some of the consorts are recognized as "first cousins"; but in most other cases they are stated to be "unrelated." If the inquiry is pressed the admission is made "were perhaps *distantly*." One may "calculate the chances" that in the same mountain community, of perhaps 300 inhabitants, who are all segregated by color from the surrounding population, two persons of the same name (uncommon outside the community) are absolutely *unrelated*, or unrelated outside the degree of seventh cousin. But even in a flat country, penetrated by a railroad, we find, as in the P. W. family, a large proportion of consanguineous marriages. The argument against the probability of unions with recessive albinism has not yet been presented with any force.

---

[26] In justice it should be added that the remark was not made in *Biometrika*.

The third point—the lack of statistical accord between the results of human breeding and those of animals—has been often remarked upon. Bateson (1909, p. 28, footnote) believes the descent of albinism in man to be complicated by some unascertained disturbance. A careful consideration and analysis of the statistics indicates, I think, that this disturbance is to be found in the method of collecting the statistics. From the matings of two persons that are simplex in pigmentation, two sorts of families are to be expected, namely, those with albinos and those without. Since in the long run, from such parents, only one albino is produced in four offspring, it is clear that the chances are that in all families of one,

TABLE XII

GIVING ALL FAMILIES CONTAINING ALBINO OFFSPRING FROM TWO PIGMENTED CAUCASIAN PARENTS

Reference.	Offspring.				Reference.	Offspring.			
	Albinic.	Pigmented.	Total.	Per Cent. Albinic.		Albinic.	Pigmented.	Total.	Per Cent. Albinic.
She.	1	3	4	25					
Enn.	7	7	14	50	Tho.	4	4	9	60
Sac.	2	1	3	67	Wil.	1	3	4	25
Don.	2	2	4	50	P-W.a.	1	11	12	8
Ed.	1	3	4	25	P-W.a. III. 15	5	3	8	62
Far.	1	5	6	17	P-W.b. II. 2	2	7	9	22
Fer.	1	3	4	25	P-W.b. IV. 3	1	2	3	33
Hlo.	2	1	3	67	P-W.c. I. 1	1	0	1	—
Hor.	1	5	6	17	P-W. VI. 1	1	3	4	25
Huf.	1	5	6	17	P-Wd. III. 11	1	0	1	—
Lie.	1	0	1	—	P-W. IV. 1	1	12	13	7
McG.	1	0	1	—	D.G.V. II. 1	4	1	5	80
McK.	2	1	3	67	D.G.V. IV. 5	1	2	3	33
Moo.	1	1	2	50	D.G.V. VI. 10	2	8	10	20
Nea.	1	1	2	50	D.G.V. V. 24	1	3	4	25
Nog.	3	4	7	42	Men.	1	0	1	—
Ria.	3	2	5	60	Man.	6	3	9	67
					Totals.	64	107	171	374

two or three children albinism will not appear. Even in families of four or more the possible case of albinism may fail to occur. All such cases of an actual low ratio of albinism are omitted from any calculation of proportions; chiefly the accidentally high ratios are brought under consideration. The actual proportions of albinos to all offspring of two pigmented parents are given for each family in Table XII.

These 33 families together with two not plotted in the diagrams are summarized in Table XII.

TABLE XIII

THE PROPORTION OF ALBINOS IN ALBINIC FAMILIES OF DIFFERENT SIZES, WHEN NEITHER PARENT IS ALBINIC

No of Children in Family.	No. Albinic.	Per Cent. Albinism.	Families.	Total Number of Families.
1	1	100	Lie., Mcg., P.W. (bis)	4
2	1	50	Moo., Nea.	2
3	2	67	Sac., Mck.	2
3	1	33	Vin., D.G.V., P.W.	3
4	2	50	Don.	1
4	1	25	She., Ed., Fer., Gur., Wil., D.G.V., P.W.	7
5	4	80	D.G.V.	1
5	3	60	Ria.	1
6	2	33	Wes.A.	1
6	1	17	For., Hor., Huf.	3
7	1	14	P.W. (not platted)	1
7	3	42	Nog.	1
8	5	63	P.W.	1
9	6	67	Man.	1
9	4	44	Tho.	1
9	2	22	P.W.	1
10	2	20	D.G.V.	1
12	1	8	P.W.	1
13	7	54	Enn.	1
13	1	8	P.W.	1
				35

Taking Table XIII in its entirety there is an average of 44 per cent. albinos to a family where expectation is 25. If we consider only the families with four or more children we find the average proportion of albinos to be 34 per cent. If we take families with six or more children the average proportion of albinos falls to 32 per cent.; with 10 or more children to 23 per cent. On the average, with the larger families the proportion of albinos tends to approach expectation.

A second source of error is not to be neglected. When the attention of the parent or acquaintance is focused by the questioner upon albinos the albinic children are all recalled, while some normal children (such as were still-born or died in infancy) are more apt to be forgotten. I have repeatedly had the experience of bringing to mind by further questioning children that had not been at first mentioned, and they were always normal children. The records of families with only one child and that an albino are frequently due to the fact that the peculiar child is the only one recalled. Considering the high frequency of infant mortality the omission of normal children forms an important factor tending to raise the proportion of albinos.

A third possible source of error lies in imperfection of dominance, *i. e.*, the occasional failure of the pigment to show itself in the young chlidren who have it simplex. Of this imperfection there are all degrees. Thus the albinos in the LIE (No. 14) and MOO (No. 17) families have a dark retina with white hair, washed-out blue iris and nystagmus. In other cases, such as the RID family (No. 20) and P-W,A (XII, 24, 25), the hair is yellowish, while the retina is pink, or the pinkish retinal glow and nystagmus may be slight. Another fact that favors the view of frequent failure of the simplex determiner to activate fully is the progressive increase in pigmentation shown by some albinos. This is a common phenomenon. Seligsohn in Eulenburg's "Real Encyclopädie," 1880, p. 162, states: "Bei einem vongesunden Eltern mit allen Merkmalen einer Albino geborenen Kinde schwand die rothe Farbe der Iris von Jahr zu Jahr." This increase in development of a simplex character has been observed by Lang in snails, by one of us in poultry and by others.

In concluding this discussion of the causes of the aberration in the proportion of albinos I wish to urge that what is needed in these studies is not so much a vaster number of families as more families that have been completely and accurately studied. Human pedigrees, like breeding records, are full of imperfect statements. The whole truth is to be gained only by visiting the families and carefully cross questioning them.

VII. Conclusions

What conclusions can be drawn from a study of the foregoing study of albinos?

1. Two albinic parents have only albinic offspring. This holds for the families Nos. 1–3, comprising four children altogether. These cases were all given us by Mr. R. R., an intelligent and reliable albino. He married an albino and had one son still, or until recently, living; albinic like his parents. These cases are, so far as I know, the first that have been published.

Dr. R. A. Gortner tells us that he formerly knew of a family of two albino parents and five albino children near his home in Nebraska, but attempts to trace this family have proved unsuccessful. The probability that this rule will hold generally is enhanced from experiments on animals where two albinos always yield only albino offspring.

2. Even when neither parent of albinos is an albino they are apt to be related. In 33 such families 11 are almost certainly from consanguineous matings. This is 33 per cent., a proportion that is certainly vastly greater than that of the population at large.[27] The fact that consanguinity even when present must frequently be unknown heightens the probability that parents of albinos are usually related. The importance of this conclusion is that it tends to bring these cases under the general rule that a recessive condition appears only when both parents carry the same defect; and the probability that both carry the same defect is heightened when both belong to the same strain.

---

[27] Lagleyze (1907) finds in 48 families of albinos consanguinity in 10, with collateral antecedents in 7, non-consanguinity in 26, and unknown 5.

3. The proportion of albinos in any family probably accords in the long run with Mendelian expectation, as in other mammals. From two non-albinic parents the proportion for families of four or more children is 34 per cent. albinos instead of the expected 25 per cent. But various causes result in an omission of normal individuals and tend to swell the proportion of the abnormal. When one parent is albinic and albino offspring occur at all we get (Rid and 4 cases in P. W.), a total of 16 albinos and 15 pigmented, which accords with expectation.

Station for Experimental Evolution,
Cold Spring Harbor, N. Y.,
September 8, 1910.

F. LITERATURE CITED

1867. Agassiz, L. and E. C. A Journey in Brazil. 540 pp., Boston [The edition cited is that of 1891].

1909. Bateson, W. *In:* Heredity and Disease. *Proc. Royal Soc. of Medicine,* II [pp. 22–30 of reprint].

1909. Davenport, G. C. and C. B. Heredity of Hair Color in Man. *American Naturalist,* XLIII, 193–211, April.

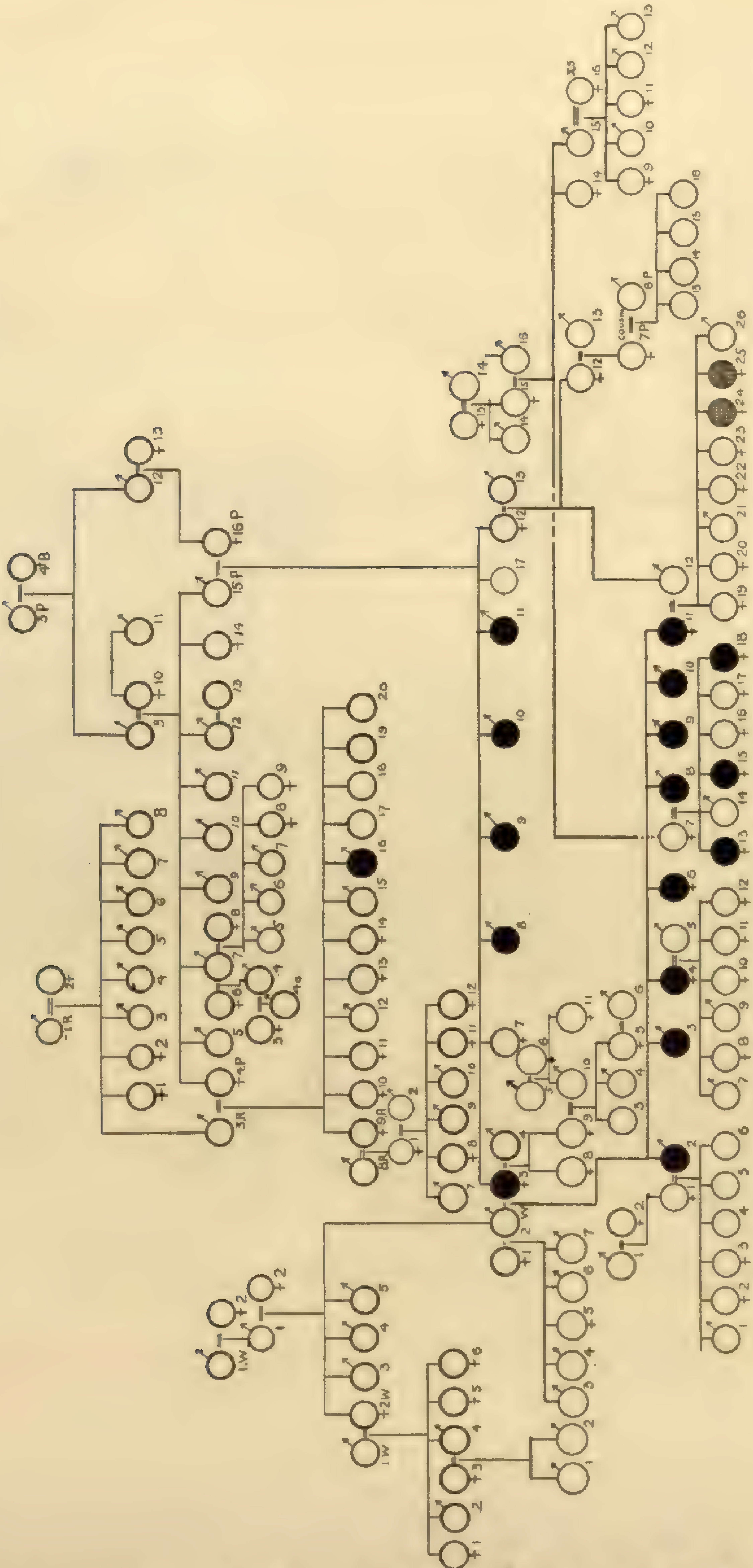
1896. Ehrmann, S. Das melanotische Pigment und die pigmentbildenen Zellen des Menschen und der Wirbelthiere in ihrer Entwickelung nebst Bemerkungen über Blutbildung und Haarwechsel. Bibliotheca medica Abth D^{II}, Hft. 6, 80 pp., 12 Taf.

1907. Lagleyze. L'oeil des albinos. Arch. d'ophthalmologie, XXVII, p. 280.

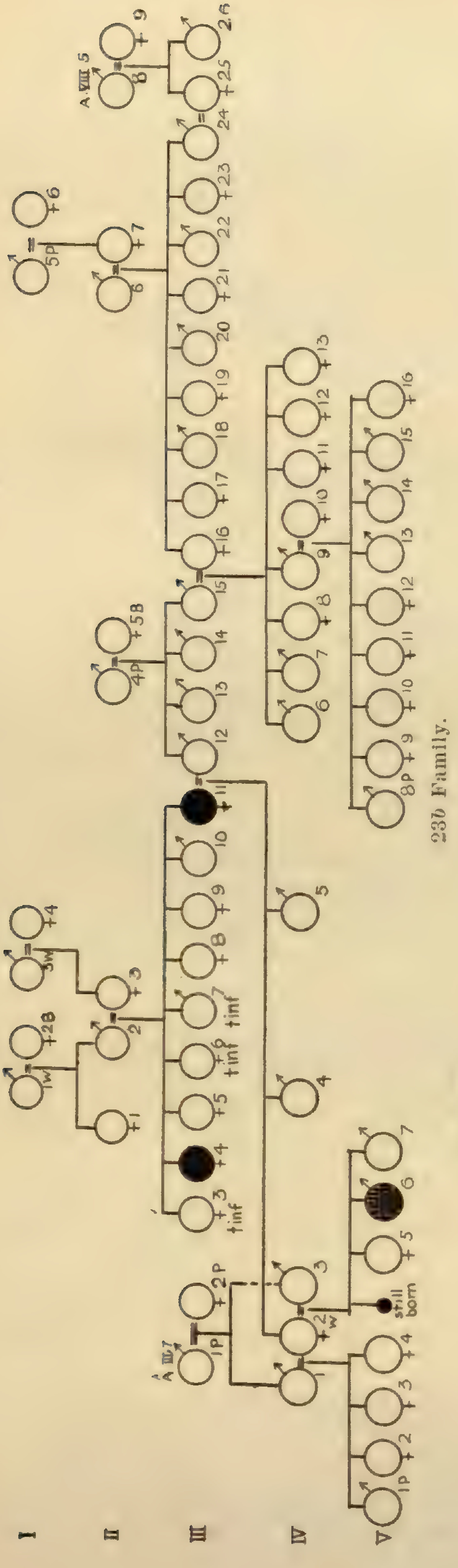
1909. Pearson, K. Note on the Skin Color of the Crosses between Negro and White. *Biometrika,* VI, 348–353, Pl. 1, March.

1909. Pearson, K. *In:* Heredity and Disease. *Proc. Royal Soc. of Medicine,* II, pp. 54–60.

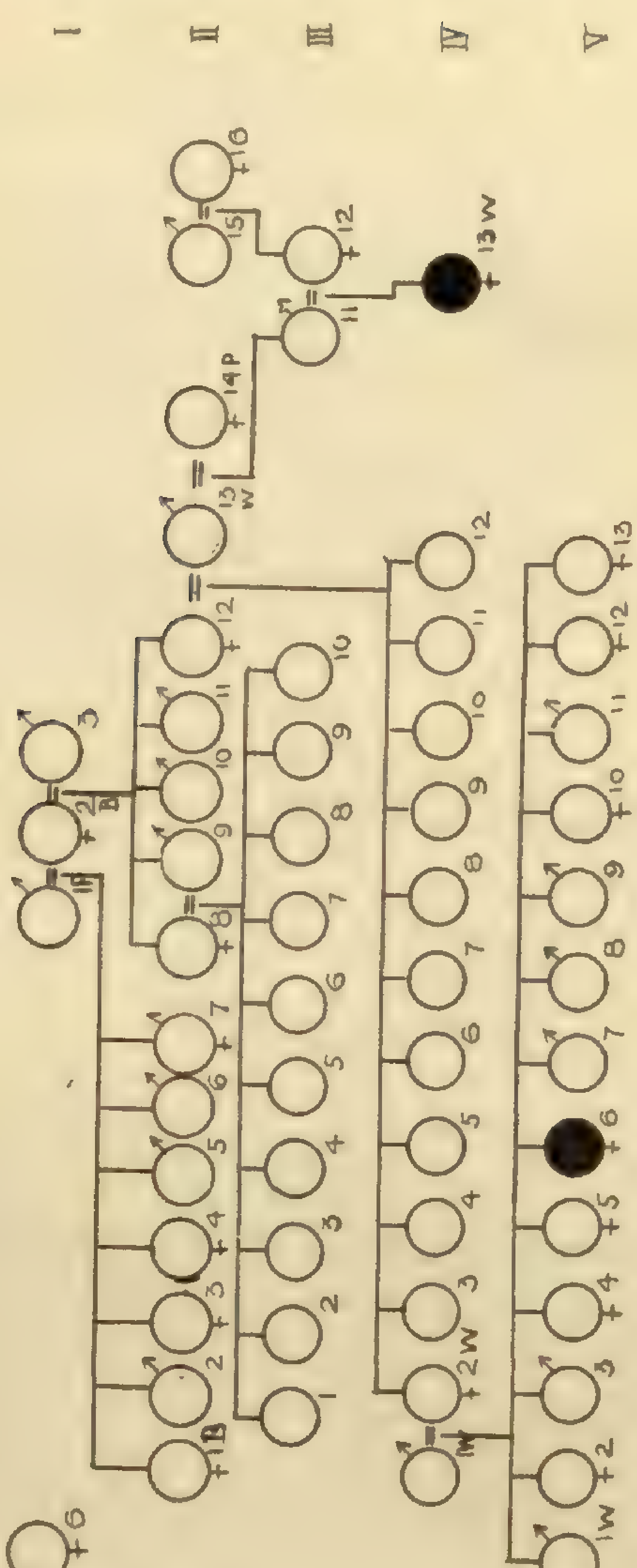
1905. Young, H. B. *Illinois Medical Journal,* XII, 201.


I
II
III
IV
V
VI
VII
VIII
IX
X
XI
XII

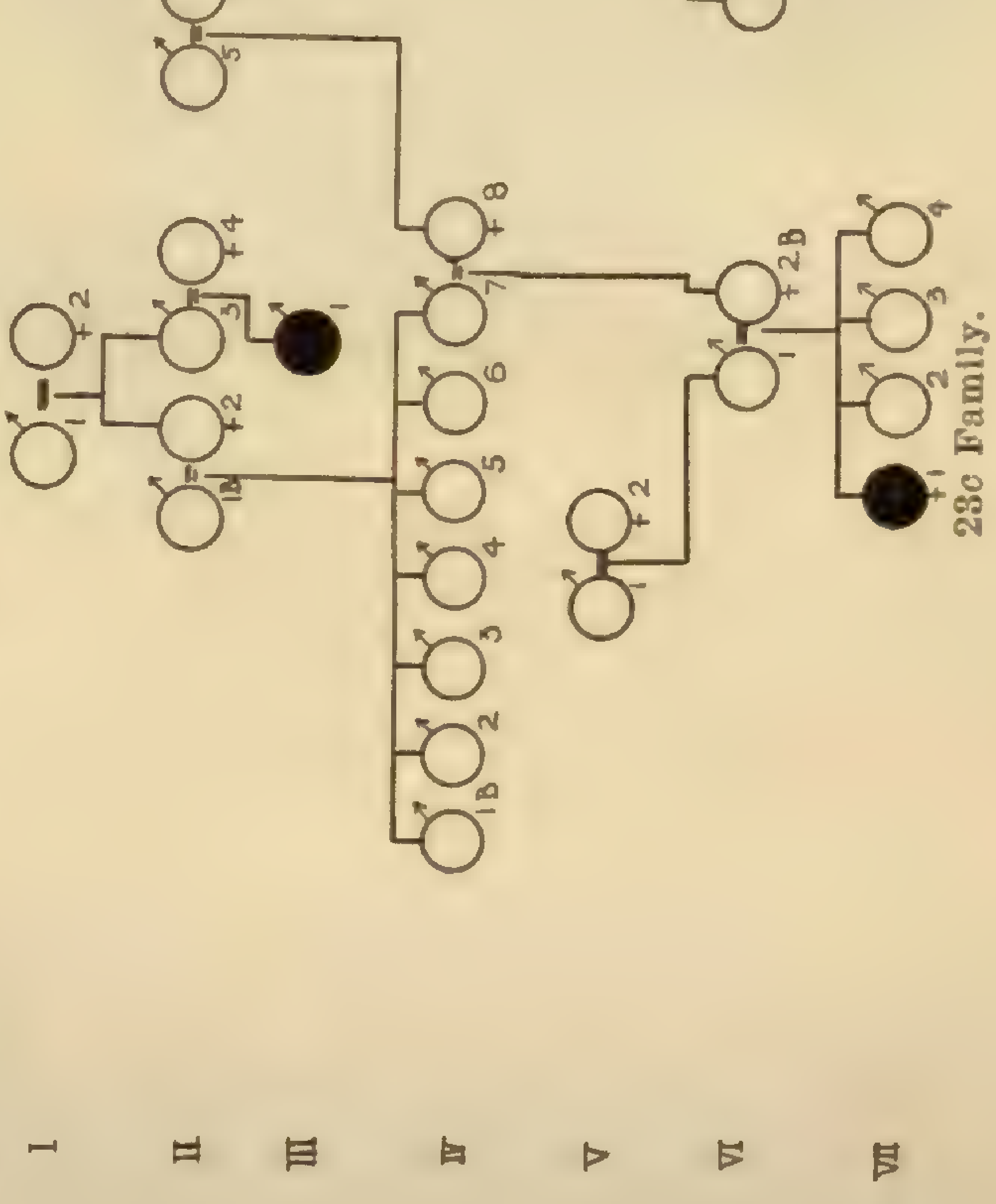
23a Family.


I
II
III
IV
V
A III 7
A VIII 5
still born
†inf

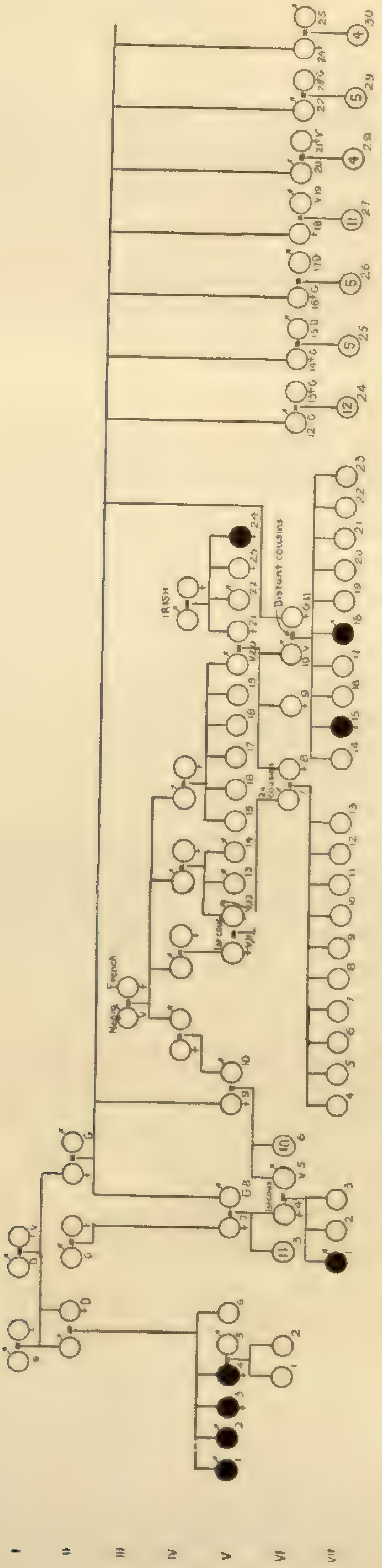
23b Family.



23d Family.


I
II
III
IV
V
VI
VII

23c Family.


I
II
III
IV
V
VI
VII
Negro
French
IRISH
Distant cousins
1st cousins
2d cousins

D. G. V. Family

SPAWN AND LARVA OF AMBYSTOMA JEFFERSONIANUM

PROFESSOR W. H. PIERSOL

UNIVERSITY OF TORONTO

SPAWN

AMONG the various accounts of the habits and spawn of *Ambystoma punctatum* occasional mention may be found of *Ambystoma jeffersonianum* but always in such connections as to suggest that *A. jeffersonianum* is by far the less common species in the locality. This along with the considerable similarity existing between the spawn of the two species may explain why no account of the spawn of *A. jeffersonianum* has as yet appeared. Descriptions of the spawn of *A. tigrinum* sufficient for distinguishing it from that of the other two species is given by B. G. Smith (1907).

In most localities near Toronto *A. punctatum* is a much more common species than *A. jeffersonianum,* however in one piece of woodland that is quite isolated from all the others examined, the former species is rarely to be found, while the latter is very abundant. This woodland contains four pools that last throughout the year, although they become heavily choked by vegetation during the late summer and autumn. The value of these pools as a collecting ground for spawn, *Branchippus,* etc., was discovered some years ago by my colleague, Dr. Huntsman and his observations on the *Ambystoma* spawn suggested to him the possibility of distinguishing in it two kinds. Later the writer also became familiar with this woodland in connection with observations on *Plethodon* and with the consent of Dr. Huntsman undertook also the investigation of the *Ambystoma* spawn of the pools.

The writer first visited these pools in spawning time three years ago and found a small amount of spawn of a type already familiar to him for some years from its abundance in pools in other localities. But the greater amount was of a type that differed from this in the points detailed below. These two types have proved to be the *punctatum* type and the *jeffersonianum* type, respectively. The predominance of the latter subsequently found its explanation in the fact that 31 of the 33 individuals captured in the woodland since then have been of the latter species. It is impossible to determine accurately the proportions in which the two types of spawn occur, but estimating roughly, the *jeffersonianum* type is at least ten times as abundant as the other.

As will appear below, a small percentage of the eggs of *A. punctatum* will approach in size, or color, or mode of deposition—but rarely in more than one of these points at a time—the eggs of *A. jeffersonianum.* Consequently, the separation of the latter as a type when found in a pool where the *punctatum* spawn greatly predominates, is not an obvious thing. But when the proportions are reversed, as in the special pools mentioned, the distinction is most easily made. Observations in the field have agreed in all four seasons and have been supplemented by the capture of females just previous to egg-laying and comparison of mature ovarian eggs and eggs laid by them in the laboratory, with those obtained in the pools; and finally by the rearing in the laboratory of larvæ from the two types of spawn.

The points of difference in order of constancy are as follows:

1. *Size.*—The eggs of *A. jeffersonianum* are distinctly the smaller, the usual diameter being 2–2.25 mm.

2. *Color.*—The eggs of *A. jeffersonianum* are much the darker, the pigment being but little removed from a true black and covering a much larger proportion of the surface of the egg than in *A. punctatum;* even the lower surface is usually as dark as the upper surface of many of the eggs of the latter species.

3. *Time of Laying.*—The deposition of most of the

spawn by *A. jeffersonianum* precedes that by *A. punctatum* by a few days. It has been impossible to visit daily the pools where the spawn of *A. jeffersonianum* is most abundant, owing to their distance from the university; one pool much nearer has yielded a small amount of it and has provided more accurate although more scanty data. In general the deposition of the bulk of the *jeffersonianum* spawn coincides with that of the first *punctatum* spawn. Variations from this occur—for instance, this year the spawn in the single pool just mentioned followed the above rule, while in the group of four pools nearly all the *jeffersonianum* spawn had been deposited three days before any *punctatum* spawn appeared; and to complete the irregularity the last spawn of all to be deposited was that of *A. jeffersonianum*. It was in small quantity and probably all from one female. (These eggs and the larvæ from them were unusually small, the larvæ seemed vigorous, but could not be kept alive many days after their own supply of yolk was exhausted.) Another check on the time is furnished by the spawning of *Rana sylvatica*. This year—an unusually early season—the writer observed the first deposition of spawn in these pools by the wood-frog. It began at 10.30 A.M., March 31. Spawn of *A. jeffersonianum* had appeared seven days previously.

4. *Spawn-masses.*—The typical spawn mass of *A. jeffersonianum* is a small one, the number of eggs being usually about twenty; the extremes encountered have been small masses of jelly without any eggs and a mass containing forty-one. *A. punctatum* does indeed deposit masses of spawn containing as few eggs as this, but the number is usually much larger. The complement of ripe ovarian eggs carried by two females of average size was 128 and 161. These are probably representative numbers and indicate a rather smaller complement than that possessed by *A. punctatum*—130 to 225—(Wright and Allen, 1908) which in turn is much smaller than that of *A. tigrinum*—1,000 or more (Powers, 1907).

5. Hardly less characteristic than the small masses is

the manner in which they are frequently to be found attached in succession to long slender twigs, each mass being usually in contact with its neighbors. A sentence in one paper on *A. punctatum* (Wright, 1908), "one stem—had within a length of one and a half feet 14 bunches of eggs, 15–20 eggs to the bunch," reads very much like a description of spawn of *A. jeffersonianum*. Many stems so laden have been found each year in the special pools mentioned. The largest piece in Fig. 1 is a portion of one of them. The twigs selected by *A. jeffersonianum* are, as a rule, very slender. *A. punctatum* will make use of both stout and slender twigs indifferently, and no small quantity has been found attached to the margins of leaves and to grass, even in the presence of such twigs as are generally preferred. Eggs of *A. jeffersonianum* have not been found except attached to twigs or stems of water plants.

The low vitality of much of the spawn of *A. jeffersonianum* is a feature that has been noticed in each year. No accurate estimate of the proportion that dies has been made, but judged roughly by the conditions found in the pools it is probably not overstating the loss to say that three fourths of the eggs do not live to begin gastrulation. The same proportion of loss has occurred in spawn reared in the laboratory, while spawn of *A. punctatum* brought from the same pools a little later and kept under the same conditions has suffered practically no loss. The egg does not die, as a whole, but cells here and there precede, the others going on dividing as usual one or more times, only to die at last. The surface view of such an egg when death is complete shows an irregular mingling of minute cells with many others two or three times as great, and at intervals others even up to eight or ten times as great, in diameter. These dead eggs imbibe considerable water, and become very much larger than the living ones and under natural conditions are soon infected by fungi; but in the laboratory they have been kept for weeks and have remained free from it; showing that death has not been caused by a fungus that only later becomes visible. All the eggs of a mass either die or develop properly; one or two of the eggs may prove exceptions to this, but whatever the defect may be it involves practically all the eggs of a bunch. Whether it may extend to all the eggs of a female it has not been possible to determine. This loss has also been observed in spawn of *A. jeffersonianum* from a second locality and is not likely to be due to any quality of the water, for in the pools of each locality spawn of *A. punctatum* has been found developing with very little loss, and that apparently due to infection by fungus. Neither can it be ascribed to low temperatures from early deposition, for the earliest is no more liable to die than that which comes later along with or after the spawn of *A. punctatum.*

LARVA

Spawn of *A. jeffersonianum* brought to the laboratory has been allowed to develop and the larvæ fed until the larger specimens had attained a length of 30–40 mm. In these it has been possible to detect a peculiarity of marking not present in similar larvæ of *A. punctatum.* This peculiarity consists of a massing of dark chromatophores into three or four spots placed in a row along each side of the mid-dorsal line, giving the animal, when viewed from above, the appearance of being banded (Fig. 2). Viewed from the side the same can be detected, but is less conspicuous (Fig. 3). Incipient banding is often indicated as soon as the chromatospheres are well differentiated (Fig. 4).

In looking over a large number of larvæ all gradations will be found between individuals in which the above shows distinctly and those in which it is impossible to detect it. For example, in 115 laboratory-reared larvæ examined at one time, 80 (69 per cent.) showed the distinctive marking. Of the balance, some individuals under different conditions showed it also (either extreme expansion or contraction of the chromatophores obscures the pattern), but some never did. Exact numbers for this division of the 31 per cent. are not available.

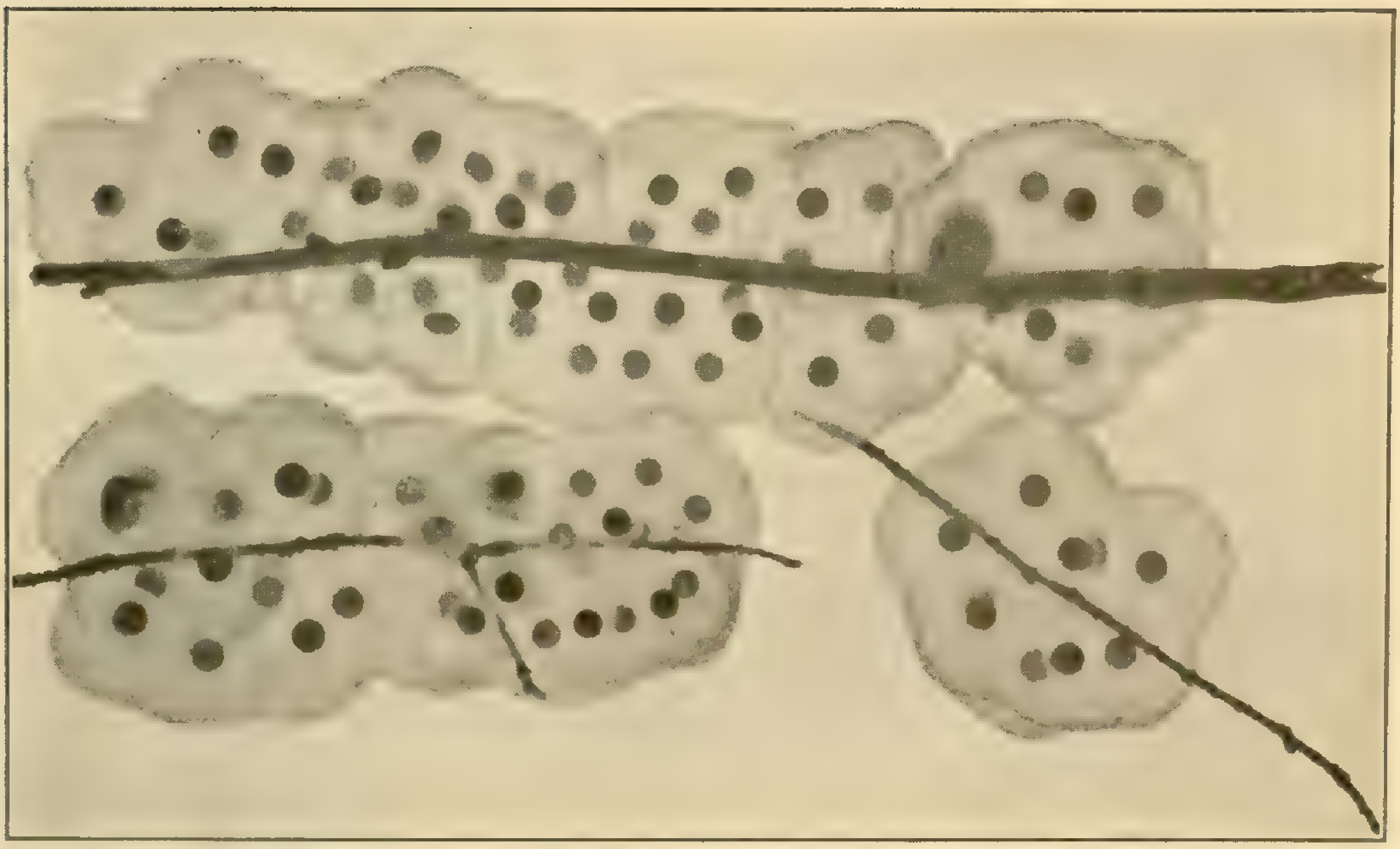


FIG. 1. Spawn of *A. jeffersonianum.* Natural size. The eggs of some of the masses are dead, others are in various stages from blastopore to medullary groove formation.

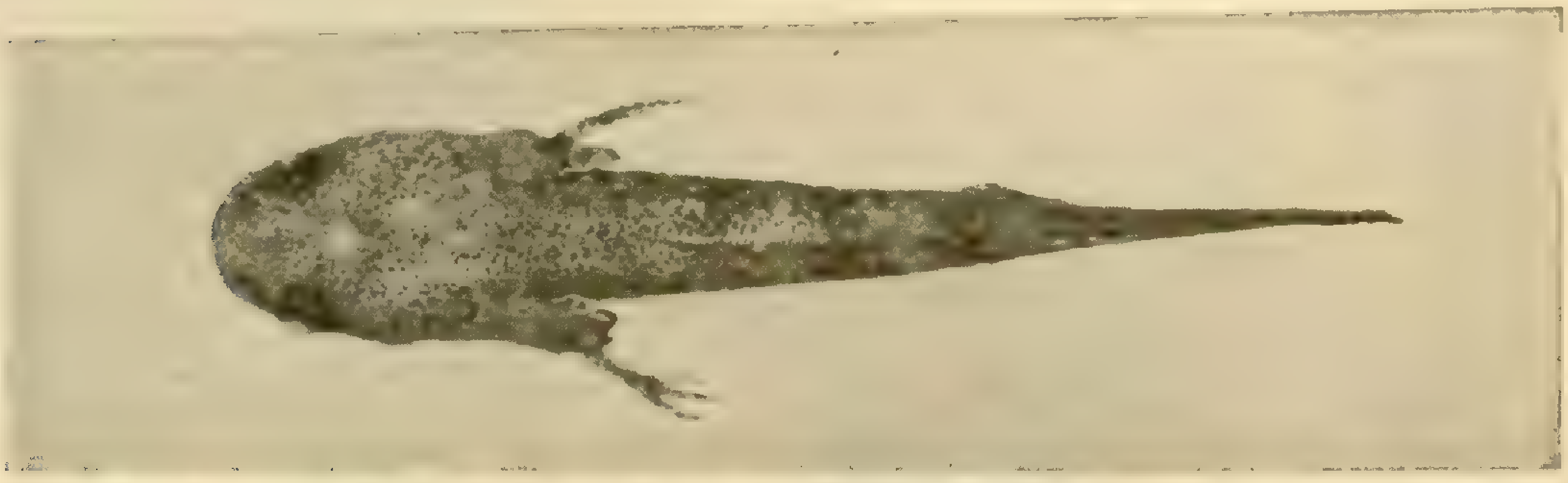


FIG. 2. Larvæ of *A. jeffersonianum.* Enlarged three diameters. Chromatophores considerably but not extremely contracted.

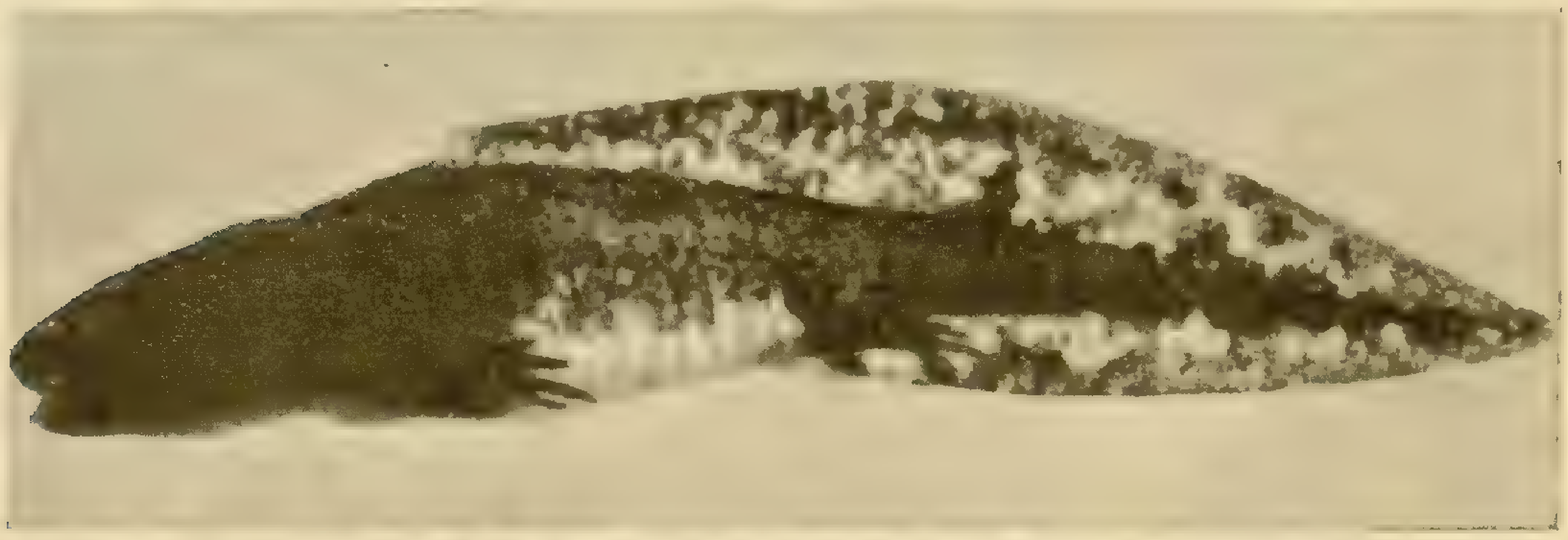


FIG. 3. Larva of *A. jeffersonianum.* Enlarged three diameters. Chromatophores considerably but not extremely expanded. The viscera and right side of the trunk have been dissected away and the photograph taken by both direct and transmitted light.

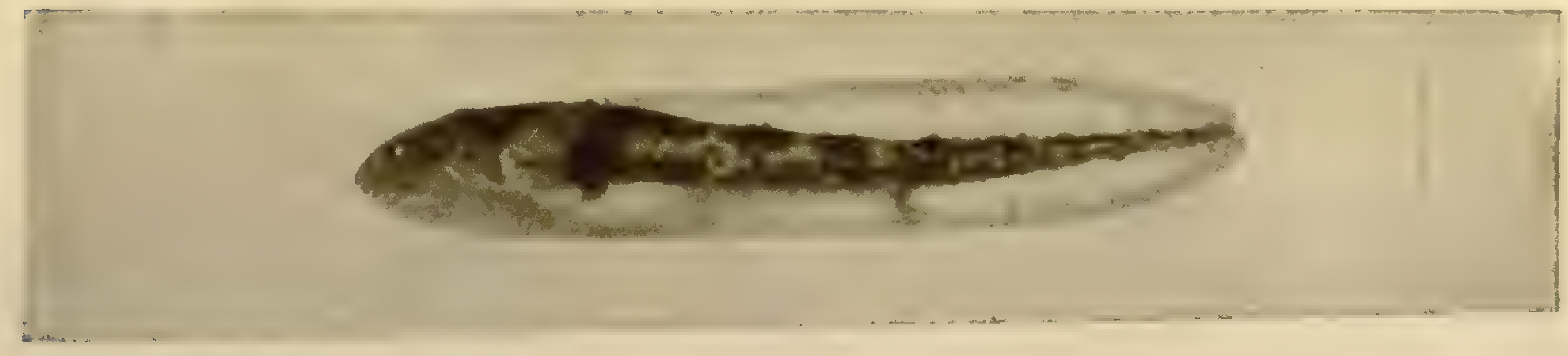


FIG. 4. Larva of *A. jeffersonianum.* Enlarged four diameters.

This year an attempt was made to remove all the spawn of *A. punctatum* from the special pools. In the middle of June larvæ 30–35 mm. long were collected from them and examined as to this pattern; it was found in but 35 per cent. Two causes may have contributed to this—the abundance of brush in the pools may have caused some spawn of *A. punctatum* to be overlooked, and the great expansion of the chromatophores—much greater than ever attained in the laboratory, the pools being very dark, probably disguised it in some cases. It was found impossible to put these larvæ under observation in the laboratory to test this point, for owing to the long journey or to the change of water they invariably died within a few hours.

Little importance would have been attached to a point of coloration so variable as this had it not been found to be uniformly lacking in similar larvæ of *A. punctatum,* whether raised in the laboratory or taken from the pools known to contain little, if any, spawn of *A. jeffersonianum.* In view of the range of coloration for *A. tigrinum* as larvæ (indicated by Powers), the degree of constancy noted is perhaps the most that could be expected.

PAPERS CITED

Powers, J. H., 1907. Morphological Variation and its causes in *Amblystoma tigrinum. Univ. of Nebraska Studies,* Vol. 7, No. 3.

Smith, Bertram G., 1907. The Breeding Habits of *Amblystoma punctatum. Amer. Nat.,* 41, pp. 381–390.

Wright, Albert H., 1908. Notes on the Breeding Habits of *Amblystoma punctatum. Biol. Bull.,* Vol. 14, pp. 284–289.

Wright, Albert H., and Allen, Arthur H., 1909. The Early Breeding Habits of *Amblystoma punctatum. Amer. Nat.,* Vol. 43, pp. 687–692.

THE INHERITANCE OF SIZES AND SHAPES IN PLANTS

A PRELIMINARY NOTE[1]

PROFESSOR R. A. EMERSON

UNIVERSITY OF NEBRASKA

SOME years ago Lock reported a cross of a tall race of maize with a shorter race which produced an intermediate height in F_1 and exhibited no segregation in F_2 when crossed back with one of the parents.[2] Castle's results with rabbits are very similar to those of Lock with maize. Castle summarizes his results in part as follows:[3]

> A cross between rabbits differing in ear-length produces offspring with ears of intermediate length, varying about the mean of the parental ear-lengths. . . . A study of the offspring of the primary cross-breds shows the blend of the parental characters to be permanent. No reappearance of the grand parental ear-lengths occurs in generation F_2, nor are the individuals of that second generation as a rule more variable than those of the first generation of cross-breds. . . . It seems probable that skeletal dimensions, and so proportions of skeletal parts, behave in general as blending characters. The linear dimensions of the skeletal parts of an individual approximate closely the mid-parental dimensions.

From his own work with rabbits and Lock's work with maize, Castle offers this somewhat guarded generalization:[4]

> It is probable that in plants, as well as in animals, linear dimensions are in general blending in their inheritance. . . . The obviously blending inheritance of height in this case [maize] does not contradict the known Mendelian behavior of the growth habit in such plants as the

---

[1] This paper was presented, in substance, in a lecture before the section of plant physiology of the Graduate School of Agriculture, Ames, Iowa, July 8, 1910. The complete records are to be published later by the Nebraska Agricultural Experiment Station.

[2] Lock, R. H., *Ann. Roy. Bot. Gard. Paradeniya,* 3 (1906), p. 130.

[3] Castle, W. E., et al., Carnegie Inst., Pub. No. 114 (1909), pp. 35, 43.

[4] *Loc. cit.,* pp. 43, 44.

sweet pea. . . . Dwarfness is plainly such a discontinuous variation in plants as is hypophylangia in man, and its inheritance is quite different from that of ordinary variations in height. The former is a discontinuous variation, Mendelian in its inheritance; the latter belongs to a series of continuous variations, and is blending in its inheritance.

While, in case of most of the crosses that I have studied where the parents differ in size, the F_1 individuals show an intermediate size, in no case have I observed anything corresponding to Castle's results with rabbits or Lock's results with corn. In every case with which I am acquainted, there has been segregation of size characters in F_2 following a "blend" in F_1. The cases in which this behavior has been studied most carefully are: size and shape of fruits of summer squashes and gourds, varieties of *Cucurbita pepo;* size and shape of bean seeds, *Phaseolus vulgaris;* size of grains and height of stalks of *Zea mays.*

Size of Maize Grains.—Queen's Golden pop corn, having small grains, was crossed with Black Mexican sweet corn, having grains of medium size. The grains of F_1 plants are intermediate between the parents in size and show no more variation in size than do the grains of the parent plants.[5] F_2 grains, as regards size, while uniform for any one plant, show marked variation between different plants. The actual measurements can not be reported at this time, but an examination of the material on hand shows that there are some ears with grains fully as large as those of Black Mexican, others with grains quite as small as those of Queen's Golden, still others whose grains are about the size of the F_1

---

[5] On ears of F_1 plants of this cross there are of course about three smooth starchy grains to one wrinkled, sugary grain. While, on account of "double fecundation," the endosperm, like the embryo, of F_1 plants is to be regarded as F_2, exhibiting the ordinary F_2 segregation, the size of grains is a plant character and to be regarded as F_1. The wrinkled grains are apparently of practically the same size as the smooth ones, though there is probably considerable difference in weight between the two lots. In a study of weights, where one parent is sugary and the other starchy, it would be advisable to use only the starchy grains of F_1 plants, and for the sugary parent only starchy, "xenia," grains produced through cross-pollination by the starchy parent. It would doubtless be better, however, to avoid this difficulty by the use of only starchy or only sugary parents.

grains, and finally grains intermediate in size between F_1 and each of the parents. What will happen in F_3 can not be told until this season's crop has been studied.

Height of Maize Stalks.—Tom Thumb pop corn is the smallest variety of maize that has come to my notice and is fully as early as any I have seen. Plants, as grown at Lincoln in 1909 and 1910, averaged about 90 cm. in height, and had on the average about eight nodes. In 1909 they ripened in seventy days from planting. This dwarf early race was crossed with a late dent corn obtained from Missouri. The stalks of the latter are above medium height for dent varieties grown in this section, though in the dry seasons of 1909 and 1910 they have reached an average height of only about 225 cm. The average number of nodes is about nineteen. The plants failed to ripen fully in 1909, owing to late planting, but were within perhaps a week of full maturity at the time of the first frost, 120 days after planting. The F_1 plants, as grown in both 1909 and 1910, are as uniform in height as either parent, with an average height of about 182 cm. (about 25 cm. above mid-parental height) and an average number of nodes of about 12 ($1\frac{1}{2}$ nodes below the mid-parent). In 1909 the F_1 plants ripened in about 100 days from planting (practically the mid-parental season). The F_2 plants (about 250 are now growing) range in size from that of the Tom Thumb parent to above that of the F_1 plants. No plant, however, is so tall as the large dent parent. While records have not as yet been made of heights, number of nodes and earliness in case of all plants, there is apparently little correlation between height and earliness. Some of the earliest plants are above medium height and some of the latest are very short. As to correlation between number of nodes and height and between number of nodes and earliness, nothing can now be said.

Size and Shape of Summer Squashes.—A cross of Yellow Crookneck and White Scallop has been grown, and F_1 and F_2 studied in small numbers. The fruit of

Crookneck has a long neck with a bowl of only medium diameter. Scallop has very flat fruits. F_1 is intermediate in both dimensions and therefore also in shape, *i. e.*, in ratio of length to breadth. F_2 shows a complete series of dimensions and of shapes from one parent to the other. The mean dimensions and shapes and the coefficients of variation in sizes and shapes for parents, F_1 and F_2 are given in the following table.

Race or Hybrid.	Means.			Coefficients of Variation.		
	Length, cm.	Diameter, cm.	Shape, L : D.	Length, Per Cent.	Diameter, Per Cent.	Shape, Per Cent.
Crookneck	39.6	11.4	3.47	17.0	12.0	13.8
Scallop	7.4	17.8	.41	15.8	12.6	26.8
Mid-parent	23.5	14.6	1.94[6] 1.60[7]	16.4	12.3	20.3
F_1 Hybrid	17.5	17.5	1.00	19.0	12.6	26.0
F_2 Hybrid	19.6	13.2	1.48	42.7	42.5	58.8

Size and Shape of Gourds.—A cross of Striped Spoon gourd with Filipino Horned gourd has been studied.[8] The Spoon gourd has a small, relatively long fruit. The relation of length of the whole fruit to the diameter of the bowl is similar to Crookneck squash. The Horned gourd has a short, relatively thick fruit. The ratio of length to breadth is greater than in case of Scallop squash. The following table gives the mean sizes and shapes and coefficients of variation in size and shape of the parents, F_1 and F_2.

Race or Hybrid:	Means.			Coefficients of Variation.		
	Length, cm.	Diameter, cm.	Shape, L : D.	Length, Per Cent.	Diameter, Per Cent.	Shape, Per Cent.
Horned	10.3	9.0	1.14	9.4	9.9	10.9
Spoon	14.0	4.2	3.36	15.6	16.0	11.8
Mid-parent	12.2	6.6	2.25[9] 1.85[10]	12.5	12.9	11.4
F_1 Hybrid	12.9	5.6	2.27	15.8	15.7	13.4
F_2 Hybrid	15.7	5.5	2.87	37.5	21.2	40.7

[6] Mean of parent shapes.

[7] Shape of mid-parent.

[8] Most of the work with this cross is being done by F. W. HofMann, a graduate student in plant breeding at the University of Nebraska.

[9] Mean of parent shapes.

[10] Shape of mid-parent.

Size, Shape and Weight of Bean Seeds.—Numerous crosses of beans differing in size and shape of seeds have been under observation. In only a few cases, however, have exact measurements been made. It will be sufficient to report here combinations of three races: Fillbasket Wax with large flat seeds; Longfellow with long, slender seeds; and Snowflake Navy with small round seeds. The mean dimensions, shapes and weights and the coefficients of variation for parents, F_1 and F_2, are given in the tables below. The parent races and the F_1 plants from which these records were taken were grown in the garden at Lincoln in 1909. The F_2 plants were grown in a greenhouse during the following winter. The different generations are not, therefore, perfectly comparable. In general the various races of beans and F_1 plants that have been grown from time to time both indoors and out have not been observed to exhibit greater variations when grown in the greenhouse than when grown in the garden, though the dimensions and weights of seeds are often noticeably larger in case of greenhouse-grown plants.

In case of the beans, summer squashes and gourds, the mean dimensions and shapes of both F_1 and F_2 are, with some exceptions, more or less like those of the mid-

MEANS

Race or Hybrid.	Weight, c. g.	Length, mm.	Breadth, mm.	Thickness, mm.	L : B	L : T	B : T
Longfellow	**28.3**	**12.9**	**5 6**	**4.6**	**2.3**	**2.8**	**1.2**
Snowflake	**16.4**	**8.3**	**5.7**	**4.7**	**1.5**	**1.8**	**1.2**
Mid-parent	**22.4**	**10.6**	**5.7**	**4.7**	**1.9**	**2.3**	**1.2**
F_1 Hybrid	**18.4**	**10.1**	**5.7**	**4.3**	**1.8**	**2.4**	**1.3**
Fillbasket	**32.2**	**13.8**	**7.6**	**4.4**	**1.8**	**3.2**	**1.7**
Longfellow	**28.3**	**12.9**	**5.6**	**4.6**	**2.3**	**2.8**	**1.2**
Mid-parent	**30.3**	**13.4**	**6.6**	**4.5**	**2.1**	**3.0**	**1.5**
F_1 Hybrid	**28.4**	**13.0**	**6.5**	**4.7**	**2.0**	**2.8**	**1.4**
F_2 Hybrid	**36.8**	**14.1**	**7.0**	**5.0**	**2.0**	**2.9**	**1.4**
Fillbasket	**32.2**	**13.8**	**7.6**	**4.4**	**1.8**	**3.2**	**1.7**
Snowflake	**16.4**	**8.3**	**5.7**	**4.7**	**1.5**	**1.8**	**1.2**
Mid-parent	**24.3**	**11.1**	**6.7**	**4.6**	**1.7**	**2.5**	**1.5**
F_1 Hybrid	**25.4**	**11.4**	**6.4**	**4.5**	**1.8**	**2.5**	**1.4**
F_2 Hybrid	**28.6**	**11.3**	**6.9**	**4.8**	**1.6**	**2.3**	**1.4**

COEFFICIENTS OF VARIATION

Race or Hybrid.	Weight, Per Cent.	Length, Per Cent.	Breadth, Per Cent.	Thickness, Per Cent.	L : B Per Cent.	L : T Per Cent.	B : T Per Cent.
Longfellow	6.09	3.27	3.57	4.54	0.61	1.76	2.46
Snowflake	9.40	2.89	3.68	5.38	2.97	5.74	4.29
Mid-parent	7.75	3.08	3.63	4.96	1.79	3.75	3.28
F_1 Hybrid	9.19	1.11	2.84	1.69	3.18	4.35	3.73
Fillbasket	7.93	3.22	2.20	3.78	3.39	6.00	3.85
Longfellow	6.09	3.27	3.57	4.54	.61	1.76	2.46
Mid-parent	7.01	3.25	2.89	4.16	2.00	3.88	3.16
F_1 Hybrid	7.63	3.53	1.43	3.37	3.35	2.55	2.95
F_2 Hybrid	17.43	8.83	10.33	9.45	7.61	12.88	13.10
Fillbasket	7.93	3.22	2.20	3.78	3.39	6.00	3.85
Snowflake	9.40	2.89	3.68	5.38	2.97	5.74	4.29
Mid-parent	8.67	3.06	2.94	4.58	3.18	5.87	4.07
F_1 Hybrid	9.90	3.47	2.70	3.83	1.29	5.04	7.06
F_2 Hybrid	24.48	8.32	5.96	8.95	7.26	39.74	9.01

parents. The most noticeable feature of the records, however, is the coefficient of variation in F_2 as compared with the parents and with F_1. The coefficient of variation is not, on the whole, materially greater for F_1 than for the parents. In F_2, on the contrary, it is noticeably greater than in F_1. It is usually twice and in some cases six or seven times as great as in F_1. This is merely a mathematical way of expressing the fact that the F_2 individuals exhibit marked segregation of size and shape characters. If the intermediates seen in F_1 were tending to breed true as blends, the coefficients of variation for F_2 would not be appreciably greater than for the parents and for F_1. This segregation in F_2 is so pronounced as not to need statistical treatment for its proper appreciation. Even a casual examination of the material can not fail to impress one with the fact that about all grades from one parent to the other are represented in F_2. As a matter of fact, some individuals among the F_2 gourds are decidedly larger than either parent.

If such results as those reported here are to be "explained" by assuming that variation is increased (in some mysterious way?) by hybridization, we can doubtless also explain, in the same way, why this increase in variation is deferred until F_2. While predictions can not be made with much assurance before F_3 has been studied, it seems probable, nevertheless, as suggested by East,[11] that we shall eventually find that sizes and shapes are not simple characters, but that a particular mean size in reality depends upon two or more, perhaps upon several, distinct factors, a part, or all, of which exhibit incomplete dominance. If this were true, we should expect intermediates (blends) in F_1 and a range of variation from one parent to the other, or sometimes even beyond the parents, in F_2 just as we do find in case of many plant characters. It should also follow that certain F_2 sizes breed true in F_3 while others continue to break up, the variation in some cases extending over the same range as in F_2 and in other cases over variously restricted ranges. There is some evidence that this suggested behavior in F_3 occurs not only in regard to size characters, but also in case of certain colors where blends are seen in F_1, but observations are as yet too meager to be presented.

I am of course not unmindful of the many chances for mistakes in interpretation of the facts secured in a study of size and shape characters. In the apparently simple cases of height of maize stalks or of bean plants, it must be remembered that parents differing in height may also differ in number of nodes, so that segregation in the latter character might bring about differences in height. Number of nodes and average internode length must both be studied instead of merely the product of these, actual height. Or perhaps, parents can be found that differ in height but have the same number of nodes. Confusion resulting from increased fluctuations due to differences in soil and season can be lessened by growing some plants of all generations to be studied in the same season (from seed kept for the purpose or by repeated crosses), and on as uniform soil as can be had. Even in the same summer plants with different periods of development may be subjected to very different weather conditions. This is of so much importance in maize, for instance, that I am now beginning a study of size inheritance of crosses between parents differing greatly in size but only slightly in earliness.

---

[11] East, E. M., Amer. Nat., 44: 72, 73 (1910).

There may possibly be definite correlations between different dimensions, as length and breadth of the same plant part. That is to say, shapes may be definitely inherited. Observations on F_2 bean seeds where the parents differ in size but not in shape indicate that length and breadth are probably not inherited independently of each other. Large round beans crossed with small round ones do not give any long slender beans in F_2 but only large, medium and small, round ones. On the other hand, when the parents differ in shape as well as in size, intermediate and parental shapes as well as intermediate and parental dimensions occur in F_2.

In short, the inheritance of sizes and shapes is not the simple matter that the inheritance of, say, color is—and recent developments indicate that color inheritance is not always a simple three-to-one affair. It is certainly well that most effort has first been directed to a solution of some of the more simple problems of genetics. Without a knowledge of the later studies in color inheritance, one could scarcely hope to get far in the investigation of the inheritance of dimensions, weights and shapes, to say nothing of such questions as whether "yield Mendelizes," which some are impatient to have answered at once.

It has been the purpose of this paper to present a few facts and to suggest many problems with the hope that the attention of other students of genetics will be directed to an interesting and important field not much worked as yet.

SHORTER ARTICLES AND DISCUSSION

THE MODIFICATION OF MENDELIAN INHERITANCE BY EXTERNAL CONDITIONS

A WHOLE number of the *Biological Bulletin* (May, 1910) is devoted to Professor W. L. Tower's article on "The Determination of Dominance and the Modification of Behavior in Alternative (Mendelian) Inheritance by Conditions Surrounding or Incident upon the Germ Cells at Fertilization." The work was done on certain chrysomelid beetles, *Leptinotarsa signaticollis, L. undecimlineata* and *L. diversa,* all occurring in Mexico. Every biologist who takes any interest in questions of heredity will read this exceedingly important paper, and will be profoundly impressed by the data therein presented, but it is possible that he will also be somewhat puzzled. It is in a humble frame of mind that I venture to set forth some of the difficulties, fully realizing that Professor Tower, with his long experience in patiently investigating the chrysomelid beetles, must know what he is about, and that any mere outsider is at a tremendous disadvantage. At the same time, it is after all for the outsider that the paper is written, and it is due to him to make it as clear as possible, and it may be to explain what seem to him insuperable difficulties.

L. signaticollis ♀ was crossed with *diversa* ♂, giving in F_1 about half *signaticollis* and half a blend between the two. The F_1 *signaticollis* mated together gave only *signaticollis,* and further breeding for five generations gave only the same. The blend, however, split in F_2 into *signaticollis,* the blend, and *diversa,* giving the expected Mendelian ratios. (The obvious suggestion here would be that the original male *diversa* was heterozygous, gametically identical with the blend.)

Next, the same cross was again made, using beetles of the same stock but at a reduced temperature. As a result, the F_1 beetles were of one sort only, the blend; and these, when inbred, gave in F_2 a typical Mendelian grouping. These two crosses were repeated eleven times with substantially the same results.

It is to be noted here that *signaticollis* appears to be a form of lower altitudes than *diversa,* and it seems possible that under the reduced temperature the pure *signaticollis* perished, leaving only the heterozygous individuals, giving the stated results. Were this the case there would be no real modification of inheritance. So far good, but now we come to the next group of experiments. Another cross was made, *signaticollis* ♀ × *diversa* ♂, under the same conditions as the first experiment, giving the same results. Then the *same beetles* were used again, at reduced temperatures (as in the second experiment above), and gave in F_1 only *signaticollis*, and this, inbred, continued true for four generations. This experiment was repeated seven times with uniform results. It seems astonishing that the cross in the first set of experiments at a lower temperature should give only the blend, and in the second only *signaticollis*. This, however, is not only explicitly stated, but is illustrated by plates showing the pedigrees of the beetles. In spite of all this there *must* be something wrong, because on page 295 it is stated that the results of the second group of experiments *confirmed* those of the first, and on page 304 it is said that the results of the second were "in every way the duplicate" of those of the first. On page 330 experiment H. 410 (the first group, at the lower temperature) is said to have given beetles exactly like the female parent (*signaticollis*), which subsequently bred true!

Is it possible that the description of H. 410 (p. 294) belonged to something else and was accidentally put in the wrong place when the paper was made up? If so, was the plate then made up from the erroneous description? There is no reason, of course, for doubting the accuracy of the experiments, but certainly there is something wrong with the account of them.

On page 299, in experiment H. 701, there arose a "single pearly white larva [which] gave rise to a female exactly like the parent type and four classes of larvæ." Something has dropped out here, and the statement as it stands is unintelligible.

In experiment H. 700 A (p. 296) a female *undecimlineata* was crossed with a male *signaticollis*, giving *only* the female (*undecimlineata*) type, which bred true for six generations. "The male type was as completely eliminated as if it had never existed." This was not a result of parthenogenesis, as all efforts to induce *undecimlineata* to reproduce parthenogenetically failed. Here it is interesting to note that *undecimlineata* differs principally from *signaticollis* in having fully pigmented bands on the elytra—a positive character. The larva of *undecimlineata*, however, is white, while that of *signaticollis* is bright yellow—the latter apparently the positive character. In the cross, the larvæ and adults were equally of the *undecimlineata* type, although it was shown in another experiment that the larval and adult characters were inherited independently, each of four classes of larvæ giving rise to three classes of adults, with Mendelian numbers. It was found perfectly possible for *undecimlineata* to have yellow larvæ, and for *signaticollis* to have white ones, when the right crosses had been made.

Are we to explain H. 700 A by saying that the result was a genuine hybrid, from the make-up of which was somehow rejected the superficial characters of *signaticollis?*

Another class of experiments, described as "experiments in synthesis" was productive of extremely interesting results. At Cuernavaca, Mexico, a suitable spot was planted with the proper food-plants, and stocked with 210 specimens of *signaticollis,* "from a standard location about a mile and a half distant" and 354 specimens of *undecimlineata.* These freely bred together, giving in the first generation 4,518 *signaticollis*, 11,744 mid-type, and 5,091 *undecimlineata.* Gradually, however, the *signaticollis* increased at the expense of the others, until at length it was the only form present. This looks like natural selection, and it will be noted that it occurs in a region normally inhabited by *signaticollis.* The experiment seems ideally perfect, except for the stated circumstance that there was a standard locality for *signaticollis* about a mile and a half away. From what we know of the migrations of these beetles,[1] it does not seem unlikely that the colony was overrun with immigrating *signaticollis.*

At Paraiso, in the foot hill rain forest, a locality was planted with 100 each of *signaticollis* and *undecimlineata.* This, I take it, is in the *undecimlineata* country. The result was exactly the reverse of the experiment just described—or not exactly that, for the *signaticollis* practically disappeared even in the first filial generation. Many other particulars are given, and there is an important theoretical discussion, but of course Professor Tower has still in hand a great mass of unpublished material of great value. One may hope that its appearance will not be too long delayed.

T. D. A. Cockerell.

---

[1] For example, in six years I had never seen *L. decemlineata* (the potato beetle) in Boulder, Colorado; but this year (1910) it appeared in enormous numbers, flying. The tomato plants in my garden swarmed with them.

NOTES AND LITERATURE

NOTES ON HEREDITY AND EVOLUTION

Mendel, in his investigations, found certain *Hieracium* hybrids which did not split up in the second generation. The writer several years ago suggested that the cause of this phenomenon might be found in apogamy. Ostenfeld[1] has recently shown that in a large number of species of this genus apogamy exists. It therefore seems probable that the constancy of these hybrids is due to the omission of the reduction division.

Pearl and Surface[2] have recently published some very interesting contributions on inheritance as a result of studies of crosses made between Barred Plymouth Rock poultry and Cornish Indian Games. It was found that eggs produced by the cross Barred Plymouth Rock males on Cornish Indian Game females gave a larger per cent. of fertile eggs than the reciprocal cross; also a larger per cent. of fertile eggs than either pure breed produced. The low percentage of fertile eggs in the cross in which the Barred Plymouth Rock female was used, the authors suggest, may possibly be due to unfavorable environment for Cornish Indian Game spermatozoa in the Barred Plymouth Rock oviduct.

There was also a higher per cent. of fertile eggs hatched for the hybrids than for either pure breed, this result being attributed to the greater vigor of the hybrids.

The Barred Plymouth Rock breed is one which has high egg-laying quality, while the Cornish Indian Game has low egg-laying quality. The very interesting result was obtained that hybrids produced by using Barred Plymouth Rock sires were good layers, thus showing that the high laying quality was transmitted by the Barred Plymouth Rock sire. On the other hand, hybrids produced by using Barred Plymouth Rock females did not possess the high laying quality, thus indicating that the Barred Plymouth Rock female does not transmit this quality directly. The facts appear to indicate that high egg laying quality is a sex limited factor like barring in the Barred Plymouth Rocks. Barred Plymouth Rock females would thus transmit high egg laying quality to their male offspring but not to their female offspring, while Barred Plymouth Rock males would transmit it to both sexes.

---

[1] Ostenfeld, C. H., "Further Studies on Apogamy and Hybridization of the *Hieracium*," *Zeitsch. f. Induk. Abst.*, Vol. III, H. 4.

[2] Raymond Pearl and Frank M. Surface, "Studies on Hybrid Poultry," Annual Report, Maine State Experiment Station, 1910. See also *Arch. f. Entwick. d. Organ.*, XXX, p. 1.

Shank color was also found to be a sex limited character. Both breeds have yellow shanks, though the Barred Plymouth Rocks sometimes have black pigment in the shank epidermis. In the cross Barred Plymouth Rock male on Cornish Indian Game female the progeny all have yellow shanks. In the reciprocal cross the male progeny have yellow shanks, while the female progeny have black shanks. The authors suggest that shank color behaves like barring in transmission. There is, however, evidently some difference, for here we get females showing a character not possessed by either parent. The writer would suggest, as a possible explanation of the behavior of shank color, that the chromosome which determines the female sex in the Barred Plymouth Rock probably has black shank latent and that this character is aroused into activity by the cross. The F_2 generation of this cross will probably give some important information on this point. Fortunately, these careful and indefatigable workers will continue these investigations.

In down color the hybrid chicks from the reciprocal crosses were alike but unlike either parent, being darker than the darkest parent.

The F_1 generation between pea comb (Cornish Indian Game) and single comb (Barred Plymouth Rock) gave all gradations from pea to single. There were more pea combs in some families than in others.

In body shape the males in the F_1 generation were all of the Cornish Indian Game type. The females were intermediate between the two breeds in this respect. The barred females—that is, those produced from Barred Plymouth Rock sires—were more like the Barred Plymouth Rock in body shape, and the black females more like the Cornish Indian Game.

In this paper the authors give the results of extended investigations relating to inheritance of the Plymouth Rock Barring. The paper is limited to the study of the cross between Barred Plymouth Rocks and Cornish Indian Games. The results confirm the present writer's hypothesis first published in 1908[3] concerning the method of inheritance of this character. The results obtained are consistent with the hypothesis that barring is allelomorphic to the female sex element. Thus, when male Plymouth Rocks are used in the cross only the male offspring are barred, the females being black. The plates accompanying the text show excellent illustrations of the nature of the barring, both in the pure bred Barred Rocks and in the hybrids. The hybrids are darker than the pure breeds, there being more pigment in the feathers.

Davenport has recently published an important contribution in the Carnegie Institution series on inheritance in poultry.[4] While he deals with many other characters than those relating to color, for lack of time to present an adequate review of the whole article, and because of its relation to the present subject, I give here only his results relating to color factors. The factors determined were as follows:

C = presence of color (absence of C gives albinism);
J = Jungle Fowl pattern and coloration;
N = super Melanic factor (nigrum);
X = super Xanthic or buff factor;
W = Graying (white) factor.

He found the Silkies and White Cochins both to be pure albinos having the gametic formula cJnwx.

White Leghorns were found to be grays with the formula CJNWx. This formula shows that W is an inhibiting factor which renders J and N invisible.

Black Minorcas and white-faced Black Spanish were found to have the formula CJNwx. In these breeds N obscures J, but the latter modifies the character black color.

Black Cochins were found to have the formula CINwx. In this formula I is a modification of J in which the pigmentation usually associated with J is absent.

Black Games were found to have the same formula as Black Cochins, but the pigment due to the factor N is less intense.

Buff Cochins were found to have the formula CjnwX. The author notes some variability in the degree of albinism, certain recessive whites showing specks of pigment. "The coloring enzyme may be absent to small traces."

---

[3] AMERICAN NATURALIST, Vol. 42, 1909, pp. 610–615.

[4] Davenport, C. B., "Inheritance of Character in Domestic Fowls," Carnegie Institution publication.

While the author recognizes sexual dimorphism as related to Jungle Fowl pattern, he does not work out the manner of inheritance of this factor. He probably would have done so had the birds been raised to the stage required for distinguishing this dimorphism.

Breeders of White Leghorns are frequently troubled by the appearance of a reddish sheen on the feathers. The formula of this breed gives a probable reason for this difficulty (CJNWx). It is probable that the Jungle Fowl coloration produces the effect in question. The cross between this breed and the Buff Cochin (CjnwX) gives an opportunity to get a breed of the formula CjnWx, which ought to be a pure dominant white, with no trace of coloration or pigment.

Goodale[5] has recently published a short but very interesting paper giving results of poultry breeding experiments, in which it appears that the Jungle Fowl pattern found in the Brown Leghorns, like the barring factor of the Barred Plymouth Rocks, is allelomorphic to the female sex factor. His paper also shows that while dominant white, when homozygote, is epistatic to black pigment, it is not so in the heterozygote condition of the white. It also indicates that females possessing the Jungle Fowl pattern and having Plymouth Rock white and Plymouth Rock black pigment, both in the heterozygote condition, may vary in color from black to almost typical Brown Leghorn pattern.

The progeny of females obtained by mating Brown Leghorn females with white Plymouth Rock males show no trace of the Jungle Fowl pattern or color, while the males obtained from this cross transmitted the Jungle Fowl pattern. There is opportunity here for a very interesting study. If the Jungle Fowl pattern and the barring of the Plymouth Rocks are both allelomorphic to the female sex factor, it would be very interesting to ascertain whether females can have both of these factors present in them. If so, it would show either that the female sex factor itself may be coupled with one or the other of these factors, or that the allelomorph to this factor may contain both factors coupled, or that the two factors reside in separate chromosomes both of which behave as allelomorphs to the female sex chromosome.

Castle has recently shown[6] that Miss McCracken's results in univoltinism and bivoltinism[7] are not inconsistent with Mendelian theory. The difficulty in interpretation is due to the fact that the characters in question are exhibited by one sex only. The same difficulty arises in following out the cross between white and red corn, since red shows only as an internal character.

---

[5] *Proc. Soc. Exp. Biol. and Med.*, Vol. 7, No. 5, May 18, 1910.

[6] Castle, W. E., *Jour. of Exp. Zool.*, Vol. 8, No. 2, March, 1910.

Hagedoorn,[8] in mating an albino mouse having the barring (agouti) character with a homozygous yellow female, finds the barring and the yellow color to be allelomorphic to each other. Certain yellow individuals mated to black gave only yellow offspring. It is probable that the yellow contains an inhibiting factor for black. Other yellow mice of a different shade mated to black gave black young. His results confirm those of Goodale in that he finds the bankiva pattern and color in Bantams crossed with Brown Reds to behave as if the bankiva pattern were allelomorphic to femaleness. When females of the bankiva type were used in the cross the male offspring were all bankiva and the females all Brown Red. When the cross was made in the opposite direction both sexes were of bankiva type. He also found (page 26) some bankiva females apparently homozygous for bankiva pattern. His data are not full or complete on this point.

On page 29 he reports that the cross between *Primula sinensis* and *P. stellata* gives *P. pyramidalis.* F_2 from this cross gives 25 per cent. *sinensis,* 25 per cent. *stellata,* and 50 per cent. *Pyramidalis,* although the two parent forms differ in more than one respect, the differences apparently being coupled.

The writer has frequently suggested that if a careful search were made for more cases of what Bateson has termed "false allelomorphs" they might be found to be more abundant than they are thought to be. Those cases which have been discovered show that such phenomena are not discovered usually unless one is looking for them. We have now a considerable number of cases of sexual dimorphism in which some somatic character acts as an allelomorph to femaleness. Presumably, these sex-limited characters would act as allelomorphs to each other if brought together in the same zygote. We have already referred to the barring of Plymouth Rocks and to the Jungle

---

[7] *Jour. of Exp. Zool.,* Vol. 7, No. 4.

[8] Hagedoorn, A. L., "Mendelian Inheritance," *Arch. f. Entw. d. Organ.*. Vol. 28, H. 1.

Fowl pattern as instances of this kind. When Silkies are crossed with Brown Leghorns, the latter breed introduces an inhibiting factor for the intense black pigmentation in the flesh of the Silkies, and this inhibiting factor appears to behave as if it were allelomorphic to femaleness. The inheritance of the factor is not yet fully worked out.[9] In addition to these cases we have that of melanism in *Abraxas grossulariata* when crossed with *A. lacticolor.* Black eyes in canaries when crossed with pink eyes appear to behave in a similar manner. We have already mentioned above shank color in poultry in this connection.

Dr. R. A. Gortner, of the Station for Experimental Evolution, Cold Spring Harbor, New York, in THE AMERICAN NATURALIST for August, 1910, gives results of quantitative determinations of melanin in white wool and black. He finds 1.84 per cent. in black wool and only .06 per cent. in white. He expresses the opinion that the melanin in white is a decomposition product of keratin and not a true melanin, thus disproving Riddle's assumption that dominant white is a more advanced stage of oxidation than black. He advances the theory that dominant whites are due to the presence of an anti-oxidase which prevents pigment formation, while recessive whites have neither power to form pigments nor to inhibit the formation.

Ostenfeld[10] finds that the number of chromosomes in the apogamic race of *Rosa canina* is about double the number in the normal sexual race in the same species, thus indicating that the reduction division is omitted.

It has generally been supposed that when an organism is moved from one environment to another distinctly different, there is a tendency for the type to break up. This thing has been described as "new place effect." There has been very little investigation bearing directly on this question, and most of it has related to forms more or less mixed in inheritance rather than to pure lines of the same inheritance. Data bearing on this subject are important and very much needed. An important contribution to our knowledge of the subject is found in Bulletin 128 of the Bureau of Chemistry of the U. S. Department of Agriculture. In this bulletin LeClerc and Leavitt give the results of experiments on wheat. Kubanka Wheat grown in South Dakota was distributed to stations in Kansas and California. Each year a sample from each station was sent to each of the others and grown there. A similar series of experiments was conducted with Crimean Wheat in Kansas, Texas and California. The results may be briefly stated as follows.

---

[9] "Bateson's Mendelian Principles of Heredity," pp. 81–87.

[10] *Zeitsch. f. Induk. Abst. und Vererb.*, Bd. III, H. 4, May, 1910, p. 253.

The same variety of wheat when grown at the same station, no matter what the source of the seed, showed the same characteristics, but the same variety grown at different stations showed marked differences. This result was obtained in the case of both varieties. These results are in entire accord with the results on barley secured by Dr. Albert Mann, who grew pedigree seeds of barley at a large number of stations in this country. The original seed was from Svalöf. These results have been previously referred to in these notes.

The appearance of an English edition of de Vries's "The Mutation Theory" (Vol. I)[11] gives the opportunity for many non-German readers to gain first hand knowledge of this remarkable work. It also serves to show the truly wonderful progress that has been made in the study of the phenomena of evolution since this book was originally published (1901–03).

In reading this book one can not fail to be impressed with the current misconceptions concerning its teachings. De Vries's disciples have given the phrase "discontinuous variation" a meaning quite different from that in which it is used in "The Mutation Theory." By "continuous" variability de Vries means the kind that fluctuates about a norm and thus presents a continuous series of modifications. Illustrations of continuous variability in this sense are found in ordinary fluctuating variations within pure lines. It was Quetelet who first discovered the fact that ordinary fluctuating variability gives a continuous series of variations varying in frequency inversely with their magnitude. That is, the magnitude of a given variation of this kind is governed by the ordinary laws of probability. In such variation every degree of departure from the normal is found. On the other hand, if we study a given character in a complex Linnean species consisting of several pure strains or subspecies, we find that each of the pure strains gives us a case of continuous variation—*i. e.*, of "fluctuation" about a norm which is fixed. But if we take these norms for a large number of pure strains within a species and attempt to arrange them in a frequency polygon, we find gaps not represented in the series, at least in some species. This kind of variation de Vries calls "discontinuous variation." We can all agree that there are such gaps between related forms in many cases. Thus, if we adhere to the original use of the term "discontinuous variation," there is no chance for debate about it. It is simply a name given to a series of well ascertained facts. How these gaps came into existence is another question. The change in the use of the term which has occurred since "The Mutation Theory" was written is in its application to the method by which these gaps came to exist rather than to the fact of their existence.

---

[11] de Vries, Hugo, "The Mutation Theory," Vol. I, The Open Court Publishing Co., Chicago, Ill., pp. 575.

A careful consideration of the data now at hand seems to the writer to leave little question that there are gaps between related forms which came into existence suddenly, and thus represent discontinuous variation in the more modern sense of this term. The only dispute which seems to the writer justifiable relates to the question whether all permanent evolutionary change comes about in this manner; and this question will be brought up again later in this article.

The progress made since "The Mutation Theory" was published is illustrated by the fact that in this book de Vries takes no account of the pure lines differing quantitatively with reference to a given character, such as those studied by Jennings, Johannsen, Nilsson-Ehle and others. De Vries also adheres throughout the book to the old notion that a given character can be modified quantitatively by selection, and states on page 51 that "It is to the selection of the material afforded by individual variability [fluctuation] that the origin of many improved races is due." Many other similar statements occur in the text. Recent investigations have thrown much doubt on the correctness of this view: we may say, have disproved it. All the recent careful work on the subject points to the opposite conclusion.

While in this book de Vries sets forth very clearly the idea that his "individual variation" is what we now call fluctuation, he continually confuses fluctuation with the effect of crossing. For instance, on page 100, we find the following: "All this [improvement of the sugar beet] has been done by selection of the best individuals afforded by ordinary fluctuating variation. Neither spontaneous variations nor crossings have played any part in it. We are dealing here with the process in its simplest form.'' It is far from demonstrated that crossings have had nothing to do with the improvement of the sugar beet. The consensus of opinion of most biologists at the present time is that selection can accomplish nothing except the isolation of the best strain or best Mendelian combination existing in a given population. It is hardly fair, however, to attribute to de Vries the opinions expressed ten years ago, for he would probably hold to-day that the opinions expressed concerning the effect of selection in ''The Mutation Theory'' have been proved to be incorrect. Such a position is really more in keeping with the fundamental principles involved in his theory, and I have no doubt that de Vries would fully admit that selection can not affect fluctuating variability, or at least that all of the recent evidence points in this direction.

For the purpose of discussing de Vries's fundamental theorem we may classify the various types of variation as follows: (1) Fluctuation; (2) those due to Mendelian recombinations; (3) those due to change in personnel of the chromosomes or other cell organs having a relation to ontogenetic development; (4) those due to fundamental changes in whatever material is responsible for the metabolic activities which result in development.

Fortunately, at the time ''The Mutation Theory'' was written the general facts of Mendelian recombination were recognized and are taken into account by de Vries, though, as previously stated, he frequently confuses them with other types of variation. De Vries also recognizes fluctuation, which he describes by the term ''individual variability,'' and appraises it at its true value, except, as stated above, that he credits selection with the power of producing temporary modifications by means of it.

The last two types of variability were not recognized when ''The Mutation Theory'' was written, so that they are utterly confused in this book.

Before de Vries undertook his Œnothera studies he was already committed to a theory concerning the manner in which evolutionary changes come about, and frankly states that his work was undertaken in order to find confirmation of this theory. Strangely enough, Darwin was responsible for the fundamental idea underlying de Vries's theory of mutation. It will be remembered that in attempting to explain the supposed inheritance of acquired characters Darwin formulated the theory of pangenesis, according to which each cell in the organism gives off a bud, or gemmule, which migrates to the germ plasm and in the next generation becomes responsible for the development of a corresponding cell in the new organism. De Vries drops the idea of migration of the gemmules from the organism into the germ plasm, and starts with these gemmules as permanent constituents of the germ plasm. He also makes other modifications in the nature of these bodies, and hence very properly gives them a new name, "pangenes."

I am of opinion that had de Vries taken an agricultural variety of wheat for his studies he would have been led to the development of a different theory. Unfortunately, he found the mutations for which he was looking in a species which was throwing off variants in a manner which we may well believe to be unusual. In fact, de Vries examined over a hundred species before he found one that suited him in this respect. Recent cytological investigations by Gates, Miss Lutz and others seem to justify at least the tentative assumption that the *Œnothera* mutants arise from a change in the personnel of the chromosomes. It is certain that in *Œnothera gigas* the *Lamarckiana* the number of chromosomes has been doubled. Gates has shown that in a general way the nuclei in *gigas* cells are twice the size of those of *Lamarckiana.* Other mutants have numbers of chromosomes not exactly corresponding with Lamarckiana. It is also demonstrated that in *Lamarckiana* and several of its mutants the course of events in the reduction division is abnormal. A good many of the chromosomes do not unite into bivalents in the usual manner, thus giving opportunity for all kinds of irregularities in the distribution of the chromosomes. The further fact that many of the mutants produce only a small proportion of functional gametes at least suggests that in many reduction divisions the chromosomes are distributed in such a way as to interfere with the future development of the gametes and the zygotes which would be formed from them.

If we assume that the chromosomes, because of their relation to the processes of nutrition or for other reasons, have an important influence on the course of development, and that there are irregularities in the distribution of these bodies in the reduction division in *Lamarckiana* and its offshoots, we at once find a satisfactory interpretation of the behavior of these mutants, and we can easily see how de Vries was misled by his material. He got the idea that the organism is composed of distinct and independently heritable units and that when one of these units is lost out or when a new one springs into existence we get an organism which differs in all of its characters from the parent form. He assumes that all permanent evolutionary change comes about by the introduction of new pangenes. For instance, he says:

> The contrast between these two groups of phenomena, variability (in the strict sense) [fluctuation] and mutability, becomes obvious when we imagine that properties of organisms are built up of perfectly distinct and independent units. The origin of a new unit is a mutation.

Again on page 57:

> Elementary species and forms closely allied to them are distinguished from one another not by a single feature but by all their organs and peculiarities. The difference between closely allied forms often demands long and extensive diagnosis. Nevertheless this diagnosis must be regarded as an expression of a single character, a single unit, which arose as such, and as such can be lost.

Again, on Page 61: "By mutation new characters arise all at once"; and on page 63: "Each mutation is a definitely circumscribed unit."

De Vries overlooks entirely those closely related pure lines, differing frequently only quantitatively, and in a single character, which to the writer represent what may be called normal evolutionary change. They not only do not differ in all their characters as the *Œnothera* mutants do, but their norms present a regular series coming under Quetelet's law, and thus represent "continuous variation," as de Vries defines it. Yet they are undoubtedly of true evolutionary value. Of these types Jennings says:[12]

> The work with genotypes [pure lines] brings out as never before the minuteness of the hereditary differences that separate the various lines. These differences are the smallest that can possibly be detected by refined measurement taken in connection with statistical treatment.

And again on page 145:

> That smaller hereditary differences are not described is certainly due only to the impossibility of more accurate measurements. Genotypes

---

[12] AMER. NAT., XLIV, pp. 144–145.

so differing have not risen from each other by large mutations. The genotype work lends no support to the idea that evolution occurs by large steps, for it reveals a *continuous series*[13] of the minutest differences between great numbers of existing races.

Nilsson-Ehle, in dealing with genotypes of oats, shows that the related lines can be arranged in a Quetelet curve with respect to the average length of the flowering glume,[14] as follows:

Average length of hull mm.	Number of genotypes
14–15	2
15–16	16
16–17	38
17–18	14
18–19	2

It would be difficult to imagine a better case of "continuous variation," as defined by de Vries.

To the writer it seems there can be no doubt that the type of variation illustrated by these pure lines of oats, and by the many pure lines of *Paramecium* studied by Jennings, is altogether different from that studied by de Vries, and is due to a widely different cause. In the writer's opinion, the *Œnothera* mutants are due to irregularities in the distribution of chromosomes in the reduction division, while the hereditary variations of the *Paramecium* type are due to actual changes in function (increase, decrease) of cell organs that have a relation to development. When such changes occur in the functions of chromosomes, the resulting differences obey Mendel's law; when they occur in other cell organs they do not obey this law.

De Vries simply generalized from too small a range of phenomena. There can be very little doubt that had he worked with the numerous small differences that exist in many species, such as have been the subject of later studies by others, he would have come to a different conclusion, or would have at least greatly modified his conclusions. The work with genotypes certainly points to a different cause for evolutionary change from that assigned by de Vries. Had he recognized what we may call the *Paramecium* type of mutation he certainly would not have said (p. 155):

> The assumption that human variability bears any relation to the variation that has or is supposed to have caused the origin of species

---

[13] Italics mine.

[14] *Bot. Not.*, 1907, pp. 113–140.

> is to my mind absolutely unjustified. . . . Since the beginning of the diluvial period man has not given rise to any new races or types. He is, in fact, immutable, albeit highly variable.

But even those of us who do not believe that *all* evolutionary change is saltatory, as it seems to be in the *Œnothera* mutants, can agree with de Vries that the difference between fluctuation and mutation lies in the fact that fluctuation is due to environment and is not hereditary, while, when a step has actually been accomplished in permanent evolutionary change, the norm about which fluctuation occurs is different from the old one. We can accept this doctrine even if we deny that the difference between the new and the old is not a "unit." We can not, however, accept the idea, repeatedly brought forward in this book, that "There is no question that improvement takes place in the experimental garden" (p. 110) when selecting for improvement in pure lines, or when he says "In the case of no single character can selection be relaxed" (p. 106); or when he quotes Halley (p. 111), with approval, to the effect that in improving wheat by selection, "the rate of improvement gradually falls off year by year until at the end of many years the race reaches a maximum and becomes constant. But, of course, it will not remain so if it is not subjected to continuous selection."

W. J. Spillman.

(*To be continued.*)

INDEX

NAMES OF CONTRIBUTORS ARE PRINTED IN SMALL CAPITALS

Algae, Nuclear Phenomena of Sexual Reproduction in the, Bradley Moore Davis, 513

Alimentary Canal of a Carboniferous Salamander, Roy L. Moodie, 367

Allen, J. A., The Rabbits of North America, E. W. Nelson, 57; Seton's Life Histories of Northern Animals, 124

Ambystoma, Jeffersonianum. Spawn and Larva of, W. H. Piersol, 732

Anatomical Characters in the Evolution of Pinus, Irving W. Bailey, 284

Anatomy, Comparative, of Conifers, E. C. Jeffrey, 253

Angiosperms, Nuclear Phenomena of Sexual Reproduction in, D. M. Mottier, 604

Animal Structure and Habits, 572

Araneads, The Significance of the Courtship and Secondary Sexual Characters of, Thos. H. Montgomery, Jr., 151

Archelenis, Tertiary, A. E. Ortmann, 237

Arithmetic of the Product Moment Method of Calculating the Coefficient of Correlation, J. Arthur Harris, 693

Artificial Production of the Parthenogenetic and Sexual Phases of the Life Cycle of Hydatina senta, A. Franklin Shull, 146

Artificially Produced Parental Modifications, The Appearance in the Offspring of, Francis B. Sumner, 5

Bailey, Irving W., Anatomical Characters in the Evolution of Pinus, 284

Barnacle, Stomatolepas, Commensal in the Throat of the Loggerhead Turtle, Henry A. Pilsbury, 304

Barnes, Charles R., The Nature of Physiological Response, 321

Bauer, E., Inheritance in *Antirrhinum*, 506

Beard, John, Sex in Animal Development, 245

Beaufort Fishes, E. W. Gudger, 395

Bee, Honey, Color Sense of the, John Lovell, 673

Bimodal Variation Polygon in Syndesmon Thalictroides and its Morphological Significance, J. Arthur Harris, 19

Biometrics, 308

Boring, Alice M., A Small Chromosome in Ascaris megalocephala, 249

Boulenger, G. A., Grayia, 703

Boveri, Th., Chromatin in Sex Determination, 246

Brainerd, Ezra, The Evolution of New Forms through Hybridism, 229

Bray, William L., Distribution and Movements of Desert Plants, 443

Browne, E. N., The Effects of Extirpation and of Transplantation of the Reproductive Organs of Insects, 316

Bubonic Plague, H. B. Ward, 439

Canadian Oyster, Larva and Spat of the, J. Safford, 343

Carboniferous Salamander, The Alimentary Canal of a, Roy L. Moodie, 367

Castle, W. E., Russo on Sex-determination and Artificial Modification of Mendelian Ratios, 434

Chamberlain, Charles J., Nuclear Phenomena of Sexual Reproduction in Gymnosperms, 595

Chance, The Logic of, in Problems of Genetics, Arthur S. Dewing, 567

Chromosomes and Heredity, T. H. Morgan, 449

Clark, Austin H., Probable Origin of the Crinoidal Nervous System, 243

Cockerell, T. D. A., The Miocene Trees of the Rocky Mountains, 31; Catalogue of Hemipterous Insects, G. W. Kirkaldy, 191; Warren's Colorado Mammals, 640; Davenport on the Ophidian Genus Grayia, 703; The Modification of Mendelian Inheritance by External Con-

ditions, 747; The Scales of Fishes, 185, 634
Coefficient of Correlation, Arithmetic of the Product Moment Method of Calculating the, J. Arthur Harris, 693
Color, Inheritance in Lychnis dioca 1, George Shull, 83; Sense of the Honey Bee, John Lovell, 673
Conifers, The Comparative Anatomy of, E. C. Jeffrey, 253
Crinoidal Nervous System, Probable Origin of, Austin H. Clark, 243
Cryptograms, The Nomenclature of, Species Plantarum of Linnaeus as a Basis for the Starting Point of the, W. G. Farlow, 385

Dahlgren, Ulric, The Origin of the Electricity Tissues in Fishes, 193
Daphnia, Reproduction of, The Effect of External Conditions on the, J. F. McClendon, 404
Darwin's Greatness and Darwinism's Weakness, V. L. K., 382
Davenport, C. B., The Imperfection of Dominance and Some of its Consequences, 129
Davenport on the Ophidian Genus Gravia, T. D. A. Cockerell, 703
Davenport, Gertrude C. and Charles B., Heredity of Skin Pigmentation in Man, 641, 705
Davis, Bradley M., Genetical Studies in Oenothera, 108; Nuclear Phenomena of Sexual Reproduction in the Algae, 513
Dean, Bashford, An Eighteenth Century Microscope, 302
Desert Plants, Distribution and Movements of, William L. Bray, 443
deVriesian Theory, Mendelian Phenomena without, W. J. Spillman, 214
Dewing, Arthur S., The Logic of Chance in Problems of Genetics, 567
Dinosaurs, Sauropod, Criticisms of the Restorations of, W. J. Holland, 259; Sauropodous, The Pose of the, W. D. Matthews, 547
Doflein, Lehrbuch der Protozoenkunde, Charles A. Kofoid, 379; and Hesse, on the Structure and Habits of Animals, G. H. Parker, 572
Dominance, The Imperfection of, and Some of its Consequences, C. B. Davenport, 129

East, Edward M., A Mendelian Interpretation of Variation that is Apparently Continuous, 65; Inheritance in Potatoes, 424
Edinger, L., Vorlesungen über den Bau der nervösen Centralorgane, G. H. Parker, 63
Eigenman, Carl H., Cave Vertebrates of America, 178
Electricity Tissues in Fishes, The Origin of, Ulric Dahlgren, 193
Emerson, R. A., The Inheritance of Sizes and Shapes in Plants, 739
Evolution, of New Forms through Hybridism, Ezra Brainerd, 229; of Pinus, Anatomical Character in the Evolution of, Irving W. Bailey, 284; without Isolation, John T. Gulick, 561; Elementary, V. L. K.
Experimental Evidence on the Effectiveness of Selection, H. S. Jennings, 136

Farlow, G. W., Species Plantarum of Linnæus as a Basis for the Starting Point of the Nomenclature of Cryptograms, 385
Fayûm Mammals, Schlosser on the, W. D. Matthew, 700
Fishes, Beaufort, E. W. Gudger, 395
Fluctuations, Are they Inherited? Harry H. Love, 412
Fungi, Nuclear Phenomena of Sexual Reproduction in, R. A. Harper, 533

Gates, Reginald R., The Material Basis of Mendelian Phenomena, 203
Genetical Studies on Oenothera, Bradley M. Davis, 108
Genetics, The Logic of Chance in Problems of, Arthur S. Dewing, 567
Gortner, Ross Aiken, Spiegler's White Melanin as related to Dominant or Recessive White, 497
Gudger, E. W., Notes on Some Beaufort Fishes, 395
Gulick, John E., Evolution without Isolation, 561
Guyer, M. F., The Chromosome Theory of Heredity, 510
Gymnosperms, Nuclear Phenomena of Sexual Reproduction in, Charles J. Chamberlain, 595

Hargitt, Charles W., The Spawn-

ing Habits of Hydroides Dianthus, 376
Harper, R. A., Nuclear Phenomena of Sexual Reproduction in Fungi, 533
HARRIS, J. ARTHUR, A Bimodal Variation Polygon in Syndesmon thalictroides and its Morphological Significance, 19; The Arithmetic of the Product Moment Method of Calculating the Coefficient of Correlation, 693

Ichthyology, Notes on, DAVID STARR JORDAN, 179, 634
Inheritance, Color, in Lychnis dioca 1, GEORGE HARRISON SHULL, 83; in Potatoes, EDWARD M. EAST, 424; of Sizes and Shapes in Plants, R. A. EMERSON, 739; Mendelian, Modification by External Conditions, T. D. A. COCKERELL, 747
Isolation, Evolution without, John T. Gulick, 561

Heredity, and Chromosomes, T. H. MORGAN, 449; W. J. SPILLMAN, 504, 750; of Skin Pigmentation in Man, GERTRUDE C. DAVENPORT and CHARLES B. DAVENPORT, 641, 705
HERRICK, FRANCIS H., Facts about the "Lobster Pearl," 294
Hesse and Doflein on the Structure and Habits of Animals, G. H. PARKER, 572
HOLLAND, W. J., Criticisms of the Restoration of Sauropod Dinosaurs, 259
Honey Bee, Color Sense of the, JOHN LOVELL, 673
Hunter, S. J., The Green Bug and its Enemies, 127
Hussakof, L., Goblin Sharks, 182
Hybridism, The Evolution of New Forms through, EZRA BRAINERD, 229
Hydatina senta, The Artificial production of Parthenogenetic and Sexual Phases of the Life Cycle of, A. FRANKLIN SHULL, 146
Hydroides Dianthus, The Spawning Habits of, CHARLES W. HARGITT, 376

JEFFREY, E. C., The Comparative Anatomy of Conifers, 253
JENNINGS, H. S., Experimental Evidence on the Effectiveness of Selection, 136
JORDAN, DAVID STARR, Note on Ichthyology, 179, 634
JORDAN, H. E., The Question of Sex Determination, 245

K. V. L., Darwin's Greatness and Darwinism's Weakness, 382
Kastle, J. K., The Oxidases, 510
Kauffman, C. H., Physiology of the Saprolegniaceæ, C. L. SHEAR, 573
Kirkaldy, G. W., Catalogue of Hemipterous Insects, T. D. A. COCKERELL, 191
KOFOID, CHARLES A., Doflein's Lehrbuch der Protozoenkunde, 379

Larva, and Spat of the Canadian Oyster, J. SAFFORD, 343; and Spawn of Ambystoma jeffersonianum, W. H. PIERSOL, 732
Leporidæ, North American, Nelson's Monograph of the, J. A. ALLEN, 57
Leriche, Maurice, Fossil Sharks of California, 181
"Lobster Pearl," Facts about the, FRANCIS H. HERRICK, 294
LOVE, HARRY H., Are Fluctuations inherited? 412
LOVELL, JOHN, Color Sense of the Honey Bee, 673
Lychnis dioca 1, Color Inheritance in, GEORGE HARRISON SHULL, 83

McCLENDON, J. F., The Effect of External Conditions on the Reproduction of Daphnia, 404
Mammalogy, 57
Mammals, Colorado, T. D. A. COCKERELL, 640; Fayûm, Schlosser on the, W. D. MATTHEW, 700
MARSHALL, F. R., The Age of Speed Sires, 431
MATTHEW, W. D., The Pose of the Sauropodous Dinosaurs, 547; Schlosser on the Fayûm Mammals, 700
Meisenheimer, Johannes, The Effects of Extirpation and of Transplantation of the Reproductive Organs of Insects, E. N. BROWNE, 316
Melanin, Spiegler's White as related to Dominant or Recessive White, ROSS AIKEN GORTNER, 497
Mendelian, Interpretation of Variation that is apparently continuous, EDWARD M. EAST, 65; View of Melanin Formation, W. J. SPILLMAN, 116; Phenomena, The

Material Basis of, REGINALD R. GATES, 203; Inheritance, Modification by External Conditions, T. D. A. COCKERELL, 747
Microscope, An Eighteenth Century, BASHFORD DEAN, 302
Miocene Trees of the Rocky Mountains, T. D. A. COCKERELL, 31
Modifications, Artificially produced Parental Modifications, The Appearance in the Offspring of, FRANCIS B. SUMNER, 5
MONTGOMERY, THOS. H., JR., The Significance of the Courtship and Secondary Sexual Character of Araneads, 151
MOODIE, ROY L., The Alimentary Canal of a Carboniferous Salamander, 367
Morgan, T. H., Sex Determination of Phylloxerans and Aphids, 246; Chromosomes and Heredity, 449
MORGULIS, SERGIUS, Is Regeneration a Repetition of the Ontogenetic and Phylogenetic Processes? 92
MORSE, MAX, Sterility, 624
MOTTIER, D. M., Nuclear Phenomena of Sexual Reproduction in Angiosperms, 604

Nelson, E. W., The Rabbits of North America, J. A. ALLEN, 57
Nervösen Centralorgana, Edinger's Vorlesungen über den Bau der, G. H. PARKER, 63
Nervous System, Crinoidal, Probable Origin of, AUSTIN H. CLARK, 243
Neurology, 63
NEWCOMBE, FREDERICK C., Plant Responses in the Categories of Sensitive Reaction, 333
Nomenclature of Cryptograms, Species Plantarum as a Basis for the Starting Point of, W. G. FARLOW, 385
Notes and Literature, 57, 124, 178, 245, 308, 379, 434, 504, 572, 634, 700
Nuclear, Phenomena of Sexual Reproduction in the Algæ, BRADLEY MOORE DAVIS, 513; in the Fungi, E. A. HARPER, 533; Phenomena of Sexual Reproduction in Gymnosperms, CHARLES J. CHAMBERLAIN, 595; in Angiosperms, D. M. MOTTIER, 604
Nussbaum, M., Sex Determination in Polyps, 251

Œnothera, Genetical Studies in, BRADLEY M. DAVIS, 108
Ontogenetic and Phylogenetic Processes, Is Regeneration a Repetition of, SERGIUS MORGULIS, 92
ORTMANN, A. E., Tertiary Archhelenis, 237
Oyster, Canadian, Larva and Spat of the, J. SAFFORD, 343

Parental Modifications, Artificially produced, the Appearance in the Offspring of, FRANCIS B. SUMNER, 5
PARKER, G. H., Edinger's Vorlesungen über den Bau der nervösen Centralorgane, 63; Ants, their Structure, Development and Behavior, W. M. Wheeler, 319; Hesse and Doflein on the Structure and Habits of Animals, 572
Parthenogenetic, Eggs of Hymenoptera, Do they produce only Males?, A. FRANKLIN SHULL, 127; and Sexual Phases of the Life Cycle of Hydatina senta, Artificial Production of, A. FRANKLIN SHULL, 146
Pearl, Lobster, Facts about the, FRANCIS H. HERRICK, 294
PEARL, RAYMOND, Quantitative Studies of Variation in Social Insects, 308
PEARSON, KARL, A Pickwickian Contribution to Our Knowledge of Wasps, 503
PIERSOL, W. H., Spawn and Larva of Ambystoma jeffersonianum, 732
Phylogenetic and Ontogenetic Processes, Is Regeneration a Repetition of? SERGIUS MORGULIS, 92
Physiological Response, The Nature of, CHARLES R. BARNES, 321
Physiology, Plant, 573
Pigmentation, Skin, Heredity in Man, GERTRUDE C. DAVENPORT and CHARLES B. DAVENPORT, 641, 705
PILSBRY, HENRY A., Stomatolepas, A Barnacle Commensal in the Throat of the Loggerhead Turtle, 304
Pinus, Anatomical Characters in the Evolution of, IRVING W. BAILEY, 284
Plant, Responses in the Categories of Sensitive Reactions, FREDERICK C. NEWCOMBE, 333; Physiology, 573

Plants, Inheritance of Sizes and Shapes in, R. A. Emerson, 739
Pose of the Sauropodous Dinosaur, W. D. Matthew, 547
Potatoes, Inheritance in, Edward M. East, 424
Protozoa, 379

Rabbits of North America, J. A. Allen, 57
Redfield, Casper L., The Age of Speed Sires, 306; Retroactive Selection, 564
Regan, C. Tate, Eels from the South Seas and Australia, 635; Classification of the Teleostan Fishes, 636
Regeneration, is it a Repetition of Ontogenetic and Phylogenetic Processes, Sergius Morgulis, 92
Reighard, Paul, White Fish Production in the Great Lakes, 638
Reproduction, of Daphnia, The Effect of External Conditions on, J. F. McClendon, 404; Sexual, in the Algæ, Nuclear Phenomena of, Bradley Moore Davis, 513; in the Fungi, E. A. Harper, 533; in Gymnosperms, Charles J. Chamberlain, 595; in Angiosperms, D. M. Mottier, 604
Reproductive Organs of Insects, Effects of Extirpation and of Transplantation of, E. N. Browne, 316
Response, Physiological, The Nature of, Charles R. Barnes, 321
Responses, Plant, in the Categories of Sensitive Reactions, Frederick C. Newcombe, 333
Restorations of Sauropod Dinosaurs, Criticisms of the, W. J. Holland, 259
Retroactive Selection, Casper L. Redfield, 564
Riddle, Oscar, Melanin Color Formation and its Bearing on the Mendelian Description of Heredity, W. J. Spillman, 116
Rocky Mountains, Miocene Trees of the, T. D. A. Cockerell, 31
Russo, A., Sex Determination and Artificial Modification of the Mendelian Ratios, W. E. Castle, 434; H. E. Jordan, 246

Safford, J., The Larva and Spat of the Canadian Oyster, 343
Salamander, Carboniferous, The Alimentary Canal of a, Roy L. Moodie, 367
Sauropod Dinosaurs, Criticisms of the Restorations of, W. J. Holland, 259
Sauropodous Dinosaurs, The Pose of the, W. D. Matthew, 547
Schlosser on the Fayûm Mammals, W. D. Matthews, 700
Selection, The Effectiveness of, Experimental Evidence on, H. S. Jennings, 136; Retroactive, Casper L. Redfield, 564
Sensitive Reactions, Plant Responses in the Categories of, Frederick C. Newcombe, 333
Seton, Ernest Thompson, Life Histories of Northern Animals, an Account of the Animals of Manitoba, J. A. Allen, 124
Sex Determination, The Question of, H. E. Jordan, 245; W. E. Castle, 434
Sexual Characters and Courtship of Araneads, The Significance of, Thos. H. Montgomery, Jr., 151
Shear, C. L., Kauffman's Physiology of the Saprolegniaceæ, 573
Shorter Articles and Discussion, 116, 243, 302, 376, 431, 503, 561, 624, 693
Shull, A. Franklin, Do Parthenogenetic Eggs of Hymenoptera produce only Males? 127; The Artificial Production of Parthenogenetic and Sexual Phases of the Life Cycle of Hydatina senta, 146
Shull, George Harrison, Color Inheritance in Lychnis dioca, 1, 83
Sires, Speed, the Age of, Casper L. Redfield, 306; F. R. Marshall, 431
Sizes and Shapes in Plants, Inheritance of, R. A. Emerson, 739
Skin Pigmentation in Man, Heredity of, Gertrude C. Davenport and Charles B. Davenport, 641, 705
Social Insects, Variation in, Raymond Pearl, 308
Sollas, I. B. J., Color Inheritance, 504
Spalding, Volney M., Distribution and Movements of Desert Plants, William L. Bray, 443
Spawn and Larva of Ambystoma Jeffersonianum, W. H. Piersol, 732
Spawning Habits of Hydroides Dianthus, Charles W. Hargitt, 376
Species Plantarum, as a Basis for the Starting Point of the Nomen-

clature of Cryptograms, W. G. FARLOW, 385
Speed Sires, The Age of, CASPER L. REDFIELD, 306; F. R. MARSHALL, 431
Spiegler's White Melanin as related to Dominant or Recessive White, ROSS AIKEN GORTNER, 497
SPILLMAN, W. J., Mendelian View of Melanin Formation, 116; Mendelian Phenomena without de Vriesian Theory, 214; Heredity, 504, 750
Sterility, MAX MORSE, 624
Stomatolepas, A Barnacle commensal in the Throat of the Loggerhead Turtle, HENRY A. PILSBRY, 304
SUMNER, FRANCIS B., The Reappearance in the Offspring of Artificially produced Parental Modifications, 5
Syndesmon thalictroides, Bimodal Variation Polygon in, and its Morphological Significance, J. ARTHUR HARRIS, 19

Tertiary Archhelenis, A. E. ORTMANN, 237
Tissues, Electricity, in Fishes, The Origin of, ULRIC DAHLGREN, 193
Transplantation and Extirpation of the Reproductive Organs of Insects, Effect of, E. N. BROWNE, 316
Trees, Miocene, of the Rocky Mountains, T. D. A. COCKERELL, 31

Urosalpinx, Variation in, HERBERT EUGENE WALTER, 577

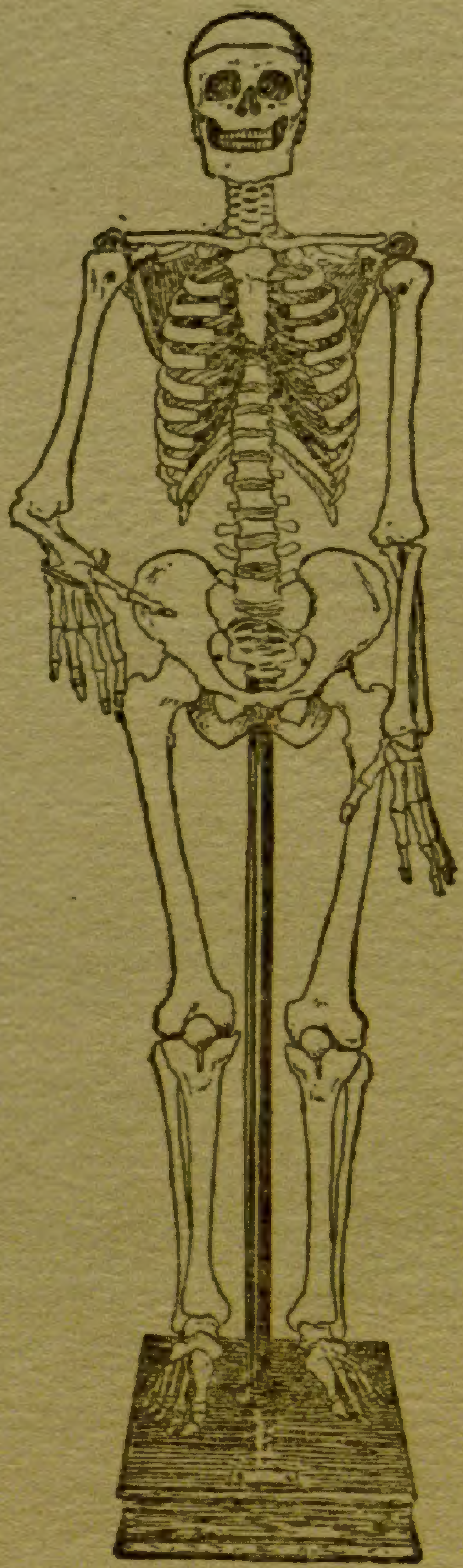
Variation, Polygon, Bimodal, in Syndesmon thalictroides and its Morphological Significance, J. ARTHUR HARRIS, 19; A Mendelian Interpretation of Variation that is apparently continuous, EDWARD M. EAST, 65; in Social Insects, Quantitative Studies of, RAYMOND PEARL, 308; in Urosalpinx, HERBERT EUGENE WALTER, 577

WALDRON, L. R., A Suggestion regarding Heavy and Light Wheat, 31
WALTER, HERBERT EUGENE, Variation in Urosalpinx, 577
WARD, H. B., Bubonic Plague, 439
Warren, E. R., Colorado Mammals, T. D. A. COCKERELL, 640
Wasps, A Pickwickian Contribution to Our Knowledge of, KARL PEARSON, 503
Webster, F. M., Toxoptera graminum and its Parasites, 127
Wheat, Heavy and Light, A Suggestion regarding, L. R. WALDRON, 31
Wheeler, W. M., The Structure, Development and Behavior of Ants, G. H. PARKER, 319
Wheldale, Miss, Color Inheritance, 504
Wilson, E. B., Chromosomes, 246

Zoology, Experimental, 316

The Anatomical Laboratory of Charles H. Ward

189 West Avenue, Rochester, N. Y.



OUR HUMAN SKELETONS are selected specimens scientifically prepared and mounted. They are undoubtedly the finest and strongest skeletons obtainable, and are purchased by the leading Medical and Literary Colleges, Schools, Surgeons, etc. We make a number of special skeletons for demonstrating dislocations, muscular areas, anthropometric landmarks, muscles, etc.

The mounting of the articulations permits movements as in life. Strength and rigidity are secured by the use of a special bronze wire of enormous tensile strength and great resistance to oxidation. Portability and ease of demonstration are attained by our nickeled steel clutch standard, which is a great protection as well.

These skeletons are shipped entirely set up, carefully wrapped, and with detailed directions for unpacking and handling. Our Catalogue gives further details.

OUR SKELETONS OF TYPES OF VERTEBRATES are large specimens, principally of American species, mounted in characteristic poses on polished mahogany pedestals, with nickel-plated brass standards. We offer a type collection for schools and colleges.

ANATOMICAL MODELS

Besides importing duty free for educational institutions we manufacture anatomical models in great variety. These have been purchased by many Schools and Universities. The series includes complete torso, head, brain, nervous system, greatly enlarged models of the sense organs, etc., of most of which we have large half tones. These models pay no duty, no transportation, no middlemen's profits, but are sold direct, at very moderate prices, and can be supplied **promptly when needed.**

We also make **BIOLOGICAL MODELS** of the forms commonly dissected in the laboratory. These models represent complete dissections of the various animals, greatly enlarged (frog 18 inches long, etc.), mounted upon ebonized pedestals, with detailed descriptive labels. Series includes Coral, Sponge, Medusa, Starfish, Diatoma, Leech, Earthworm, Clam, Crayfish, Amphioxus, Perch, Frog. Sample labels and halftones on request.

ANTHROPOLOGY AND ETHNOLOGY

The Finsch Life Masks of Aborigines, including those islanders recently acquired by the United States. Casts of Skulls, Skeletons and Brain, of Prehistoric Man. Casts of prehistoric bone carvings from the caves of France. Stone implements of the North American Indians.

RELIEF MAPS OF THE UNITED STATES, the Continents, Grand Cañon of the Colorado, Yosemite Valley, etc., made in Washington, D. C., for the United States Geological Survey and others by Howell (a former member of the Survey). **The only authoritative relief maps made commercially in America.** They are light, strong (made of papier maché), beautifully colored and lettered, and as low in price as "cheap" maps. For catalogues, halftones of models, maps, etc., address

CHARLES H. WARD

189 West Avenue, Rochester, N. Y.

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE JUNE NUMBER

The Botanical Society of America: The Nature of Physiological Response. The Late Professor Charles R. Barnes.

The Place of Plant Responses in the Categories of Sensitive Reactions. Professor Frederick C. Newcombe.

The Larva and Spat of the Canadian Oyster. Dr. J. Safford.

The Alimentary Canal of a Carboniferous Salamander. Dr. Roy L. Moodie.

Shorter Articles and Discussion: Observations on the Spawning Habits of Hydroides Dianthus. Professor Charles W. Hargitt.

Notes and Literature: *Protozoa*—Doflein's Lehrbuch der Protozoenkunde: Professor Charles A. Kofoid. Celebrating Darwin's Greatness and Darwinism's Weakness, V. L. K.

CONTENTS OF THE JULY NUMBER

A Consideration of the "Species Plantarum" of Linnaeus as a Basis for the Starting Point of the Nomenclature of Cryptogams. Professor W. G. Farlow.

Notes on Some Beaufort Fishes. E. W. Gudger.

On the Effect of External Conditions on the Reproduction of Daphnia. Dr. J. F. McClendon.

Are Fluctuations Inherited? Dr. Harry H. Love.

Inheritance in Potatoes. Professor Edward M. East.

Shorter Articles and Correspondence: The Age of Speed Sires: Professor F. R. Marshall.

Notes and Literature: Russo on Sex-Determination and Artifical Modification of the Mendelian Ratios, Professor W. E. Castle; The Bubonic Plague, Professor H. B. Ward; Desert Plants, William L. Bray.

CONTENTS OF THE AUGUST NUMBER

Chromosomes and Heredity. Professor T. H. Morgan.

Spiegler's "White Melanin" as Related to Dominant or Recessive White. Dr. Ross Aiken Gortner.

Shorter Articles and Correspondence: A Pickwickian Contribution to Our Knowledge of Wasps: Professor Karl Pearson.

Notes and Literature: Heredity, Dr. W. J. Spillman.

CONTENTS OF THE SEPTEMBER NUMBER

Nuclear Phenomena of Sexual Reproduction in the Algæ. Dr. Bradley Moore Davis.

Nuclear Phenomena of Sexual Reproduction in Fungi. Professor R. A. Harper.

The Pose of the Sauropodous Dinosaurs. Dr. W. D. Matthew.

Shorter Articles and Discussion: Evolution without Isolation, Dr. John T. Gulick. Retroactive Selection, Casper L. Redfield. The Logic of Chance in Problems of Genetics, Arthur S. Dewing.

Notes and Literature: Animal Structure and Habits, Professor G. H. Parker. Plant Physiology, C. L. Shear.

CONTENTS OF THE OCTOBER NUMBER

Variations in Urosalpinx. Dr. Herbert Eugene Walter.

Nuclear Phenomena of Sexual Reproduction in Gymnosperms. Charles J. Chamberlain.

Nuclear Phenomena of Sexual Reproduction in Angiosperms. Professor D. M. Mottier.

Shorter Articles and Discussion: Sterility, Dr. Max Morse.

Notes and Literature: Notes on Ichthyology, President David Starr Jordan. The Mammals of Colorado, Professor T. D. A. Cockerell.

CONTENTS OF THE NOVEMBER NUMBER

Heredity of Skin Pigmentation in Man. Gertrude C. Davenport and Charles B. Davenport.

The Color Sense of the Honey Bee—Can Bees distinguish Colors? John Lovell.

Shorter Articles and Discussion: The Arithmetic of the Product Moment Method of Calculating the Coefficient of Correlation: Dr. J. Arthur Harris.

Notes and Literature: Schlosser on Fayûm Mammals. Dr. W. D. Matthew. The Ophidian Genus Grayia: Professor T. D. A. Cockerell.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**